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DECOMPOSITION OF NEEDLE LITTER
IN A 120-YEAR-OLD SCOTS PINE
(*Pinus silvestris*) STAND AT
IVANTJÄRNSHEDEN

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DECOMPOSITION OF NEEDLE LITTER IN A 120-130-YEAR-OLD SCOTS PINE (*Pinus sylvestris*) STAND AT IVANTJÄRNSHEDEN, JÄDRAÅS

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Abstract

Preliminary results are presented and some conclusions are drawn from decomposition studies on Scots pine (*Pinus sylvestris*) needle litter. Weight losses of needles were measured by litter-bag technique three times annually and experiments were started in three consecutive years. Annual weight loss was found to be about 27% at the site and the weight loss was about 64% after 3 1/2 years without any fragmentation taking place. The amount of total nitrogen (Kjeldahl) and nitrogen bound to Klason lignin increased in the course of decomposition before the amount started to decrease. The different organic components of the litter started to decompose in a certain order with extractives and arabinans first and lignin last. The other components measured were cellulose, mannans, xylans, galactans, rhamnans and crude protein. When lignin weight loss started the lignin level appeared to remain about constant. Regression analysis indicated that the decomposition of the whole litter apparently took place with a constant fractional weight loss (1st order kinetics). Some of the analysis fractions decomposed similarly, namely the fractions consisting of arabinans, mannans, glucans, extractives and lignin respectively.

A rough budget for needle litter biomass was calculated.

1. Introduction

No, faith, not a jot;
 but to follow him thither with modesty enough,
 and likelihood to lead it; as thus:
 Alexander died, Alexander was buried, Alexander returneth into dust;
 the dust is earth; of earth we make loam;
 and why of that loam, whereto he was converted, might they not stop
 a beer-barrel?
 Imperious Caesar, dead and turn'd to clay,
 Might stop a hole to keep the wind away;
 O! that that earth, which kept the world in awe,
 Should patch a wall to expel the winter flow.

Hamlet in 'Hamlet, Prince of Denmark' *
 (Shakespeare, 1603)

Like the remains of Alexander and Caesar in the quotation, litters and their nutrients are transformed in the process of decomposition. The suggestion that the remains should - sooner or later - circulate and turn into a form which is useful - even if somewhat unexpected - is also close at hand for litters.

In both cases the pathways are very incompletely known but in the latter case, studies have been carried out into parts of the circulation process. The process of litter decomposition appears to be the limiting process for the release of nutrients, but comparatively little is known about decomposition of plant litter in nature. The chemical composition - both the inorganic and the organic - could be expected to be an important regulatory factor for the rate of the decomposition process and some studies have been carried out which deal with decomposition vs. the organic and inorganic composition of the litter. Melin (1928) found that the percentage of nitrogen in litters strongly affected the weight loss rate. He also suggested that the decomposition is affected by other factors, among which tannins have

been assumed to affect weight loss rate in oak leaves (Harrison, 1971). The percentage of lignin has a strong negative influence on decomposition rate and Fogel & Cromack, 1977, found it to be more rate determining than the C/N quotient or total nitrogen content.

What is rate limiting for decomposition in one system is not necessarily limiting in another and such rate limiting factors ought to be investigated. The presence of a soil fauna, including e.g. mites which cause fragmentation of the litter, possibly changes the mode and rate of decomposition as well as the limiting factor compared to a system where only microorganisms can be considered to exert activity in the decomposition process.

Decomposition of *Pinus sylvestris* needle litter has been studied to some extent. This needle litter is easy to obtain and very uniform at needle fall in autumn. The most commonly used method to study needle litter decomposition is the litter-bag method which has been found to have certain weaknesses, however (Rosswall & Berg, 1973). It could be expected that the bag would to some extent shield the litter from contact with its immediate surroundings depending on the litter-bag's mesh-size. On the other hand, litter under degradation is normally fragmented, and litter-bags would be to prefer as fragments are to some extent retained within the net structure. In the case of a soil fauna taking an active part in litter degradation the mesh-size of the litter-bag must admit passage of the animals. The forest stand studied has a soil fauna, of which few species could affect the decomposition rate in the litter-bags. The mites have been shown to cause a decrease in weight loss rate (Lundkvist, 1978). They can, on the other hand, move freely through the litter-bag net. The rate of needle litter decomposition is rather low and the complete decomposition of the fibre structure has been reported to be seven years (Kendrick & Burges, 1962). Mikola (1960) found weight loss of pine needle litter to be 43-58% in three years depending on the geographic location in Finland.

In spite of its very common use the interpretation of the word "decomposition" appears to differ widely depending largely on the scientist studying the process. It can, for example, mean just weight loss irrespective of whether compounds have been leached or metabolized. The word decomposition as used in this paper will mean weight loss of the substrate. The weight of organisms having invaded the substrate appears to be too small to be taken into account (Berg & Söderström, to be published) (Clarholm, pers. comm.). As no water soluble material was leached from the needle litter studied the phenomenon of leaching is not mentioned in the definition.

The aim of the present study was to describe the decomposition of *Pinus sylvestris* needle litter. Analyses were carried out to determine the organic composition of the remains and to obtain a useful measure of substrate quality for use in simulation models. Already in the thirties Waksman & Starkey (1931) published results showing that the cellulose and hemicellulose fractions were degraded faster than lignin (originally from a graph published by Tenney & Waksman). Swanger (1975) measured the changes in, for example, cellulose, hemicelluloses, lignin and soluble materials after 220 days' decomposition. Hayes (1965) reported that the polyphenol content of pine needle litter decreased notably during the first year of decomposition.

The present paper is the third in a series dealing with decomposition and substrate changes in needles and other litter types appearing at the SWECON study site at Ivantjärnsheden, Jädraås, Sweden. Its aim is to present the work in progress, give background material and preliminary conclusions for the purpose of decomposition modelling. It must be emphasized that the results presented and discussed in the present paper are of a very preliminary nature - and should be regarded as such. None of the measurements have been finished so far and the report simply presents the state of the work in February 1978.

2. Materials and methods

2.1 Needle collection, storage and weighing

Needles were sampled at Ivantjärnsheden in late October 1973, 1974, 1975 and 1976 and taken from the branches of about 15-year-old Scots pines. The brown needles were about to fall from the trees, all of which were located in an area less than $20 \times 50 \text{ m}^2$, and were stored at -20° until the sample preparation took place.

Before weighing, the needles were air dried at room temperature to approximately 5-8 % moisture. The biggest difference in moisture was less than $\pm 0.5 \%$ from the average.

2.2 Description of methods tested

The litter-bags were made of terylene net with a mesh-size of 1 mm and measured $8 \times 8 \text{ cm}^2$. In each litter-bag was enclosed an amount of about 2 g of needle litter and a piece of plastic tape giving the weight of the needles. The bags were fastened to the ground by 10-15 cm long metal pins.

The needles on nylon strings were split up into about 0.2 g bundles, each of which was fastened and kept together by a metal clip covering a 2 mm long piece of the needles. The needles bundles were tied together with nylon string and each such sample was laid directly on the ground.

The samples were placed on the L layer in 19 test spots ($1 \times 1 \text{ m}^2$) in the 120-year-old stand (Ih VA), series A as soon as the snow had melted - about May 5, 1974 and series B, C and D in late October 1974, 1975 and 1976 respectively just after the needle litter fall period. When the A series was started a small series of litter bags was laid under the moss layer.

When collected, (one sample from each test spot) the 19 samples were transported directly to the laboratory and cleaned of moss, lichen, and cowberry remains. At each sampling one needle was taken out per sample for determination of invading mycelium (Berg & Söderström, to be published). After drying at 85°C the sample weights were determined and chemical analysis carried out.

2.3 Chemical analysis

Samples were ground together in a laboratory mill equipped with a filter allowing particles of less than 1 mm diameter to pass. The amount of water soluble and acetone soluble substances were determined by sonicating the milled samples for three consecutive times (of 20 min. each) in a sonicator bath and weighing the samples after filtration and drying. Analysis of Klason lignin and solid carbohydrates in the needle samples under decomposition was carried out according to Betghe, Rådeström and Theander (1971). In addition, soluble lignin was determined spectrophotometrically (Schöning & Johansson, 1965). The needle litter samples from the A series were analysed by Prof. O Theander and co-workers (Berg, Hannus, Popoff & Theander, to be published) for organic components.

Analyses for nitrogen and carbon were made on the ground samples of whole needles and the Klason lignin fractions were analysed for nitrogen. The analyses were carried out at the National Swedish Laboratory for Agricultural Chemistry, Uppsala. Release of water soluble substances from whole needles was investigated by allowing the needles to soak in distilled water at room temperature for 10 and 24 h.

3. Results and discussion

3.1 Method studies

3.1.1 Weight loss rates

Two methods were tested, namely, litter-bags with the litter enclosed in terylene-bags with a mesh-size of one mm and non-confined needle bundles where the needles were fastened with metal clips. It could be expected that litter-bags would prevent the transport of needles down the moss profile and

thus change a.o. their moisture content. It appeared, however, that the weight loss rates for needle litter in the L and FH layers were not significantly different (Table 1) and it thus appears that the position in the profile had no effect on the process. There was no soil fauna active in decomposition which was excluded by the litter-bags at this site (Lohm, pers. comm.).

The needle bundle method allowed the needles a better contact with the moss and the bundles sank into the moss faster than did the litter-bags. On the other hand there was a too high weight loss with about 60 per cent after 460 days when the litter-bag method gave only about 34 per cent. When comparing these two different rates with the input to the layer and its content of needle litter the high value would not allow the amount of litter actually found in the L layer (see section 3.5). From the budget calculation it thus appears that the litter-bag method should be the most reliable of those tested. There was an observed fragmentation from the bundles - with the needles often broken at the edge of the metal clip.

3.1.2 Fragmentation

To determine the rate of fragmentation, needles were marked with a spot of white paint and laid on the moss layer. There was a very high loss per cent of needles, possibly due to the fact that the white paint simply loosened. It seemed, however, that there was no fragmentation in the first three years as all the marked needles found were unbroken but it appeared that some fragmentation had started at about three years and a half. As there was a high loss of these needles no quantification could be carried out. It can be noted, however, that the needles in the litter-bags were not fragmented after three and a half year.

3.1.3 Weight loss at the test spots within the site

Within the site studied there were no significant differences in decomposition rates among the subsites used. There appeared to be a random distribution of weight loss values between them (Table 2). The differences between weight loss values for the needle litter apparently depended on other factors than the very local vegetation and canopy cover. It seems as if in this stand each litter-bag should be regarded as a separate unit with its own weight loss rate.

3.2 Needle litter weight loss

3.2.1 Observations on the measurements started in May and October 1974. At the main study site - the 120-year-old stand - weight loss measurements with needle litter were started in May 1974 (series A), and October 1974 (series B). The main measurement was the A series, samplings of which were made at least three times annually (Table 3) together with careful chemical analysis carried out (Berg *et al.*, to be published). The chemical analyses are discussed in section 3.2.4.

It appears that the sizes of weight losses varied within the year (Figure 1). The highest weight losses took place in the period from May to November whereas in winter - from November until end of April - there was very little weight loss. The winter weight losses varied, however, probably depending on the temperature in the L layer. The relatively warm winter from November -74 to May -75 gave a relatively high weight loss with 17.7 per cent (B-series) whereas the corresponding period in 1975-76 was rather cold with an average temperature of about -4°C in the L layer (P-E. Jansson, pers. comm.) and gave rather low weight losses (Table 3). The winter 1976-77 had a higher L-layer-temperature (close to 0°) due to a thick snow cover and the decomposition increased somewhat compared to the winter before. The high weight loss of the B-series was not observed on any other occasion (Table 3). The graph describing the weight losses for this series (Figure 2) appears to be close to that for the A series.

In, for example, budget and kinetic calculations use must be made of annual weight loss figures. The weight losses obtained were sensitive to the climate conditions and samplings should be carried out preferably on the same date every year. To obtain a representative graph the points for the one-year-weight-loss values of the needle litter were connected (Figs 1 and 2). There was no leaching ($< 1\%$) from the needle litter, a fact also found by Nykvist (1963) but all the material was decomposed within the needle structure. If there had been any initial leaching of importance this ought to have been reflected in the graph, which should have cut the Y-axis slightly above the zero point. The mechanical leaching from litters by water mainly takes place within a short time period, as shown by Nykvist (1963). When the soluble substances remain within the structure they will

disappear more slowly (Berg et al., to be published) - due to microbial metabolism.

At its maximum the fungal biomass was about 5.2 mg/g needle litter (Figure 1). At this point (600 days) the weight loss was 44 per cent. The amount of mycelium was thus about 1 per cent of the weight loss which is within the standard error for the determination and this level appears to be kept during the course of the process.

As judged from the appearance and the brittleness of the needles after 3 1/2 years decomposition they might start to fragment at any time. Such fragmentation would break the graph and the measurements values would then give both mechanical humus formation and decomposition.

3.2.2 Annual variation

There were differences in weight loss between the years with weight loss values of 27, 28, 21 and 27 per cent respectively for the first year's decomposition (Table 3). The average value for the first year was thus 26 per cent.

The two-year weight loss values for series A, B and C were 45, 43 and 45 per cent and are very close (average 44 per cent). There were no differences in levels of lignin and nitrogen in the initial needle litter (see section 3.2.4) between the years and it thus appears less probable that chemical differences should have given rise to the rather low value of 21 per cent. When calculating the second year percentage weight loss for the A and B series we obtain 24 per cent for the A series (750513-760428) and 20 per cent for the B series (751028-761110). The 21 per cent decomposed in the C series needle litter in the same time period was rather close to these values, especially to that of the B series. The low value for the first year of the C series might thus be due to different climatic conditions in this year affecting all the needle litter series (see also section 3.2.1).

3.2.3 Comparison of weight losses for needle litter in the L and FH layers

Weight loss of needle litter placed on the litter and humus layers in the 120-year-old stand tended to differ (Table 1). It appears that in summer-autumn periods a higher weight loss took place for the samples

in the litter layer than for the samples in the humus layer.

The opposite situation appeared to be typical for the winter-spring periods. There were thus no differences after two years but significantly higher weight loss for litter layer samples after completed summer-autumn periods.

Changes in organic and inorganic components (see Materials and Methods) were followed. The increases in total nitrogen levels were very close for the two layers. It appeared, though, that there became more nitrogen bound to the slowly degraded Klason lignin in the humus layer needles (Table 1). Thus there was a lower amount stored in the crude protein fraction. Most of the single hemicelluloses and the Klason lignin were degraded about as fast in both layers. However, the cellulose fraction was notably higher in the humus layer needle samples suggesting a more active cellulose decomposition in those of the litter layer. The combined cellulose and hemicellulose fractions exerted a similar but less clear difference between the layers than did the cellulose fraction. In the samples of both layers the soluble components were about the same size and these fractions are probably too variable to show any significant differences.

There are differing fungal microfloras at different levels in the soil profile of this 120-year-old stand (Söderström & Bååth, 1978). This suggests possible differences in decomposition pattern of organic chemical components as it can be expected that the enzyme composition of the microflora will change between the layers.

3.2.4 Chemical changes in the needle litter under decomposition (A and B series)

It must be noted that the very careful chemical analysis carried out on the A series needle litter (Berg *et al.*, to be published) like that on the B series only reflected the states of certain analytical fractions with time. The biological and chemical background for the changes taking place are not discussed in detail only the changes measured.

3.2.4.1 Proposed major lines in the chemical changes

The data presented in Tables 4 and 5 and in Figures 3 to 7 might appear slightly confusing at first glance. However, there seem to be some main patterns in the decomposition process which, for the sake of clarity should be outlined before each substance is discussed.

- A. There was little chemical variation in the initial needle litter used in the different measurements in the A - D series.
- B. There were different weight loss rates for the different chemical components.
- C. The percentages of some of the substances decomposed, like lignin, cellulose, and mannan, increased - at least initially - in the litter during decomposition. Other substances kept at a rather even level like xylan whereas others decreased their levels almost at once, e.g. the arabinans and soluble substances.
- D. The amounts of some chemical components sometimes increased initially like for lignin which might be due to chemical processes like humification, but generally the amounts decreased from the start of the decomposition process.
- E. Both the percentages and amounts of total nitrogen and nitrogen associated to Klason lignin increased - the former possibly due to active uptake by fungi (Berg & Söderström, to be published).
- F. At 50-60 per cent weight loss it appeared that the cellulose, hemicellulose and lignin fractions attained rather constant ratios to each other. It is possible that from this point and onwards the organic chemical composition might be rather constant.

We can distinguish a sequence in which the components started to decompose.

It appears that both the arabinans fraction and the fraction of extractives started to decrease immediately. The mannans, galactans and xylans

started to decompose after some months - the mannans possibly after six months when substances like the arabinans had been degraded to about half the original amount. There was no net decrease of cellulose until after more than a year and the Klason lignin fraction started to decompose at about 700-800 days.

The different weight loss patterns were probably due to differing availabilities of the substances in the analytical fractions. The word "available" is used here in a wide sense including for instance steric and metabolic availability - the latter caused by the enzymatic patterns of the microorganisms.

The conclusions that can be drawn are still uncertain but it appears that lignin should be the substance most slowly decomposed. It could thus be expected that the rate of weight loss for lignin could determine the rate of weight loss for the other analytical fractions. Consequently we could expect that the population of microorganisms at a certain level of litter decomposition - due to sterical reasons - had to degrade the lignin fraction to be able to degrade and make use of the polymer carbohydrates. A possible consequence would then be that the chemical composition of the organic matter would become rather constant at a certain stage of decomposition. This concept is supported by the almost constant lignin level in the later stages of decomposition (Table 4 and Figure 6).

3.2.4.2 The Klason lignin fraction

The Klason lignin fraction does not consist exclusively of lignin at analysis but also of humus substances (Theander, pers. comm.). The Klason lignin fraction thus might have a turnover early in the decomposition process but as only a net value was measured it appeared to remain almost undecomposed.

The percentage of Klason lignin increased steadily during the course of decomposition (Figure 3) and after about 2 1/2 years the percentage was doubled. The total amount of Klason lignin increased notably in the first six months and was followed by a net loss first after about 800 days. After three years there was still only a small total weight loss in this fraction and the amount did not go below the initial until after more than 2 years.

The increase in amount of Klason lignin (Table 4, Figure 3) with about 10 per cent (20 mg per initially 220 mg lignin or per 1 000 mg litter) at its maximum could be due to the humification process. The increase in amount of the lignin fraction took place in the same time interval as the increase in total amount of nitrogen. The increase in lignin-nitrogen appeared to reach a maximum somewhat later than the maximum in the lignin fraction. Of the increase of 20 mg "lignin" it would appear that about 10 mg came from nitrogen adsorbed or bound to lignin (the increase measured from 0 up to 550 days).

3.2.4.3 Total nitrogen

After a slight loss of nitrogen early in the decomposition process both the percentage and the amount started to increase (Figure 3). The microorganisms in the needle litter might take nitrogen from their surroundings (Berg & Söderström, to be published) and after about eighteen months there appeared to be a maximum of 130 per cent of the initial amount, i.e. a 30% increase (Staaf & Berg, 1977). The amount then decreased but even after 3 1/2 years the amount was still greater than the initial one but was now stored in less than 400 mg litter that remained of the initial 1 000 mg. The average increase per year was roughly 22 mg added to the remaining structure of initially 1 000 mg litter. The percentage of nitrogen in the remaining litter increased all the time. It can be noted that within each year there was a clear tendency for the nitrogen percentage to increase slightly during the summer period. In the relatively short period from late August to late October a very notable increase took place (Figure 3). In the winter period (snow cover and frost) either a small increase or decrease took place.

3.2.4.4 Nitrogen associated with the Klason lignin

The percentage of lignin-nitrogen increased steadily as long as the amount of lignin was above its initial value (Figure 3). When the latter started to decrease after 2 1/2 years the percentage of lignin-nitrogen became rather constant.

The amount of lignin-nitrogen also increased steadily until the lignin fraction started to decompose. The amount of lignin-nitrogen then tended to decrease at about the same time as the percentage appeared to become constant.

The processes of humification and mineralization certainly continues during decomposition, thus leading to increases in the amount of humified nitrogen. The decrease in the amount of lignin indicated that the Klason lignin fraction had started to decompose. The graph thus showed a net value for nitrogen between these two processes.

During the phase of increase of lignin-nitrogen (from about 1 000 up to 500 days) about 50 per cent of the total nitrogen taken up into the litter became bound to the lignin fraction. This binding takes place with nitrogen in the ammoniac form (Nömmik, 1965). When 126 mg of carbon were mineralized (248 mg weight loss and 51% C) the increase of total nitrogen was 14.6 mg of which at least 7.2 became bound to lignin.

3.2.4.5 Nitrogen not associated to lignin

In the first two years the percentage of nitrogen not associated to lignin increased steadily as did the total nitrogen. There was no clear indication that changes occurred in this nitrogen fraction (Table 4) and the amount might - so far - be considered constant during the course of decomposition.

In the later stages of decomposition this fraction probably mainly consists of microorganisms. Berg & Söderström (to be published) found about 5 mg of mycelium at 1 100 days (see biomass values plotted in Figure 1).

3.2.4.6 The glucal (cellulose) fraction

The percentage of glucans increased in both series (A and B) and remained at a higher level than the initial one. This was most pronounced in the A series. The remaining amounts from 1 000 mg litter decreased - once decomposition had started - steadily down to a level where the amount in this analytical fraction appeared to be constant. There was a difference between the series, possibly depending on the higher initial amount of cellulose in the B series, and consequently a longer time was needed for the amount to decrease.

3.2.4.7 The mannan fraction

Either there was a slight increase in the percentage of the mannans (A series) or they remained constant (B series) at 7-8 per cent for a long period. At a litter weight loss of about 50-60 per cent the amount started to decrease (A series) whereas in the B series the weight loss started more or less immediately.

3.2.4.8 The galactan fraction

The percentage of galactans was fairly constant with small variations during the course of decomposition. Consequently there was an almost immediate drop in the amount. In the A series there was a delay until the degradation started. It appears that the decomposition was delayed or temporarily stopped at a litter weight loss of 50-55 per cent - as was also the case with the decomposition of glucans and mannans.

3.2.4.9 The arabinan fraction

The level of arabinans did not vary according to any distinguishable pattern. The amount decreased notably already in the early stages of decomposition in both A and B series. As with the other polymer carbohydrates, there was a delay in the later stages as the amount became rather constant.

3.2.4.10 The xylan fraction

The xylan fraction had a rather constant percentage initially and it appeared to increase with litter weight loss. The amount of xylan remaining from 1 000 mg initial litter decreased slowly at first and then was degraded quicker down to a rather constant level at about 50 per cent litter weight loss.

3.2.4.11 The rhamnan fraction

This fraction was very small and there was no distinguishable pattern in its decomposition, but this might depend on the small amounts and uncertainty in analysis. The fraction might be constant or might decrease.

3.2.4.12 The behaviour of the combined hemicellulose fraction

Values for the single components were summed to obtain a decomposition pattern for the hemicelluloses as a group. It appeared that the percentage increased slowly up to about 40-45 per cent weight loss of litter

after which it decreased slightly. The amounts of hemicellulose decreased from the beginning until a rather steady level was reached at about 50 per cent litter weight loss.

3.2.4.13 The behaviour of the total polymer carbohydrate fraction

The pattern shown by the combined glucan and hemicellulose fractions was slightly different to that of the hemicellulose fraction. The percentage increased considerably and varied from sampling to sampling. In general, the percentage remained higher than at the start. The total amount also increased initially or remained constant until 20-25 per cent litter weight loss, after which it decreased until a rather constant level was reached at about 60 per cent litter weight loss.

3.2.4.14 The behaviour of the fraction of extractable components

After an initial increase the percentage of water soluble components decreased comparatively quickly and had reached a level of 3-6 per cent already within a year, after about 25 per cent litter weight loss. The amount decreased in a similar pattern.

The acetone-soluble fraction followed much the same pattern and consequently their sum ("total extractives") also had a similar behaviour. As pointed out by Berg et al., to be published), it is possible that the fraction of extractives contained metabolites and decomposition products from the decomposing microflora.

3.2.4.15 The ash fraction

This fraction had a practically constant percentage during the course of decomposition, the amount thus sinking slowly with time.

3.3 Is the needle litter weight loss a process of constant fraction weight loss?

Some scientists have attempted to describe litter decomposition mathematically. Olson (1963) used a negative exponential function ($y=e^{-x}$) but did not present any directly measured decomposition data in support of his function and probably assumed that no leaching from the litter could take place. It appears from the discussion by Minderman (1968) that the leaching phenomenon was involved in his calculations - "decomposition

during the first year after leaf fall is very great". He points out that a negative exponential function ($y=e^{-x}$) did not show what actually happened in his decomposition system but suggests that weight losses of separate constituents should be tested for their closeness to such functions.

Bunnel & Tait (1974) used data from a system where leaching from various litters took place. They developed Olson's function and included a term for leaching. They thus separated weight loss of soluble components, leachable from the litter without any microbial activity, and weight loss of material due to biological action. Their modified equation for weight loss, as a function of time $W(t)$ is

$$W(t) = W_1 e^{-r_1 t} + W_2 e^{-r_2 t}, \quad (1)$$

where W_1 = the initial weight of the readily leached component, r_1 = average annual weight loss of the readily leached component, W_2 = the initial weight of the less readily decomposable component, the ligno-cellulose structural fraction, and r_2 = average annual weight loss of the less readily decomposable component.

While the functions of Olson (1963) and Bunnel & Tait (1974) have a theoretical - biological background it appears that the asymptotic function suggested by Howard & Howard (1974) is a result of data fitting. Some of the litter types used by them probably can leach soluble substances to a considerable degree - the ash (*Fraxinus excelsior*) leaves release up to 20 per cent of their dry weight (Nykqvist, 1963). Such a quick initial weight loss would suit the type of function suggested. The idea of a limit value for litter weight loss in the absence of soil fauna appears from a microbiological point of view unlikely. The possibility cannot, of course, be excluded that systems with such enzyme resistant structures exist, but the generality of such a function would appear to be limited.

As a consequence of the discussion above, the function (1) of Bunnel & Tait ought to be reasonable and should be the first to be tested. There

was no readily leachable fraction in the pine needles used but all substance was decomposed within the needle structure (section 3.2.1). When applying the function the term $W_1 \cdot e^{-r_1 t}$ equals zero and the function would thus be identical to that used by Olson. With the symbols above we thus get

$$W(t) = W_2 \cdot e^{-r_2 t} \quad (2)$$

A regression analysis was made with this function and the weight loss values for the needle litter weight loss in series A and B (section 3.2.1). For series A the following function was obtained with values taken from Table 14 (13 sets of values with W in per cent and t in days)

$$W(t) = 96.44 e^{-0.00079 \cdot t} \quad r^2 = 0.987*** \quad (3)$$

whereas values from Table 5 (7 sets of values) were used for series B.

$$W(t) = 98.61 e^{-0.00076 \cdot t} \quad r^2 = 0.989*** \quad (4)$$

The rather high r^2 values strongly indicate that the decomposition process followed a function of the type e^{-x} .

As seen from the dates in Tables 4 and 5 from Figures 1 and 2, the weight loss values varied within the year as discussed in section 3.2.1. The weight loss value for the winter period (April or May) and the two for the summer period (August and November) result in an overrepresentation of the latter values. The weight loss graph might thus represent weight losses that are too high. To avoid the seasonal variations a regression was run with the one-, two-, and three-year-values of decomposition indicated in Figure 1 and 2. The functions thus obtained with these values (including a weight loss of 0 at the time of 0 days) for the A series were:

$$W(t) = 98.63 e^{-0.00078 \cdot t} \quad (5)$$

and for the B series

$$W(t) = 98.77 e^{-0.00077 \cdot t} \quad (6)$$

The r^2 -values were 0.999*** and 0.994*** which, however, cannot be compared directly to those from eq. 3 and 4 because of the lower degrees of freedom. Significance levels used: ** for $p < 0.01$ and *** for $p < 0.001$.

In a type graph the weight loss value would asymptotically come close to 100% weight loss. In the process studied this point could be calculated but cannot of course be determined experimentally. Weight losses even of about 90 per cent might be difficult to determine due to the fact that when fragmentation of the litter starts no weight loss values will be reliable.

Minderman (1968) discussed whether the weight loss of single chemical components in litter would follow an exponential function and considered the phenomenon of masking which was suggested by Handley (1954). So far there does not appear to be any substances which caused disturbances in the weight loss functions. Even if the percentage of lignin increased considerably (Tables 4 and 5, Figure 3) there were no noticeable disturbances in the straight line plots (Figures 2 and 9). As seen from Figure 8 a fairly constant relation between lignin and the total litter biomass occurred fairly early and then remained unaltered. This might indicate that the decomposition process does not change but instead all components decompose at a constant rate. This might then support the validity of the function even after the point where weight loss measurements are no longer possible.

From the section above it follows that the weight loss would be considered a constant fraction of the amount remaining.

The function presented above (2) can be rewritten as

$$k \cdot t = \ln \frac{W_0}{W_t}$$

$$\text{or } k \cdot t = \ln 10 \times \log \frac{W_0}{W_t} \quad \text{where:}$$

k is a rate constant

t is time

W_0 is the initial concentration of the substance

W_t is the concentration of the substance at the time t .

When plotting $\ln 10 \cdot \log \frac{W_0}{W_t}$ against time a straight line was obtained (Figure 2 and 9).

Linear regressions of the log values for plot values (Table 6) gave for the A series the function of a straight line with

$$Y = 0.00079 X + 0.03622 \quad r^2 = 0.986^{***} \quad (8)$$

and for the B series (Table 7)

$$Y = 0.00075 X + 0.01396 \quad r^2 = 0.990^{***} \quad (9)$$

where $Y = \ln 10 \cdot \log \frac{W_0}{W_t}$ and

$X = t$ (in days)

Using a similar discussion as in section 3.2.1 I felt that regressions of the one-, two-, and three-year values plus the start value at $t = 0$ ought to be made. These gave also straight lines with rather similar equations, namely:

$$Y = 0.00078 X + 0.01379 \quad r^2 = 0.998^{***} \quad (10) \quad \text{and}$$

$$Y = 0.00077 X + 0.01241 \quad r^2 = 0.994^{***} \quad (11)$$

for the A and B series respectively.

The rate constants were $0.000813 \text{ day}^{-1}$ (0.296 yr^{-1}) for the graphic calculation (Figure 9). The regression analysis gave the value 0.288 yr^{-1} (eq. 8), 0.274 yr^{-1} (eq. 9), 0.285 yr^{-1} and 0.281 yr^{-1} (eq. 10 and 11) (Table 8).

The time for decomposition of half the amount of the needle litter (halftime) was calculated to be 2.33 years (Figures 1 and 2). The regressions for the A and B series gave 2.28 and 2.48 years respectively (eqs 8 and 9) and somewhat closer values were obtained with 2.39

and 2.42 for eqs 10 and 11 (Table 8). Although there were only few points for these latter regressions, the sets of data used were less dependent on periods with unusual weather as only weight losses for whole years were taken into account: It is possible that these values could be more useful for further calculations. Ninety per cent weight loss was calculated to take place rather close to eight years and 99 per cent at about sixteen years.

3.4 Did the weight losses of the organic components in the needle litter follow a negative exponential function?

Minderman (1968) suggested that the weight loss of single organic components in litter might follow an exponential function although the total litter weight loss did not do so. Such a suggestion appears reasonable and I carried out a test with the analysis values from needle litter, series A, to check the theory.

As seen from Figures 3-6 and from Tables 4 and 5 the decomposition of the different organic components started at different points of time. The amounts of some components were constant for some time before decomposition started. The time factor was thus set to zero until decomposition (or a net weight loss) started. Regression analyses on the type function e^{-x} were carried out with analysis fractions with values that were not too scattered, namely the combined values for water soluble and acetone soluble fractions ("total extractives"), the glucan fraction, the arabinan fraction, the mannan fraction, and the Klason lignin fraction. The sum of the hemicelluloses and the sum of total polymer carbohydrates were also tested.

It must be pointed out and stressed that the results presented were the first in a series of similar calculations to come from the needle litter decomposition series A, B, C, and D and my intention was thus not to put forward very specific functions for the different components and combined fractions. The variations in the initial composition of the needle (Berg, to be published) were of such a magnitude that the functions presented below, (1) - (7) must be regarded with care. More evaluations of ongoing research are necessary, before reliable conclusions can be drawn about the possible validity of such functions. Some general conclusions have, however, been made and are discussed below.

The combined fraction of extractives (Table 9) gave:

$$(1) \quad W(t) = 84.8 e^{-0.001284 \cdot t} \quad (12 \text{ pairs of values})$$

$$r^2 = 0.826***$$

where $W(t)$ is remaining amount of the fraction

t is time in days from the day when decomposition of the fraction started.

A graphic representation of the function is shown in Figure 10.

The arabinan fraction (Table 10) gave:

$$(2) \quad W(t) = 75.6 e^{-0.000103 \cdot t} \quad (12 \text{ pairs of values})$$

$$r^2 = 0.897***$$

A graphic representation of the function is shown in Figure 11.

The mannan fraction (Table 11) gave:

$$(3) \quad W(t) = 100.9 e^{-0.001180 \cdot t} \quad (8 \text{ pairs of values})$$

$$r^2 = 0.959***$$

A graphic representation of the function is shown in Figure 12.

The glucan fraction (Table 12) gave:

$$(4) \quad W(t) = 94.2 e^{-0.001130 \cdot t} \quad (10 \text{ pairs of values})$$

$$r^2 = 0.823**$$

A graphic representation of the function is shown in Figure 11.

The Klason lignin fraction (Table 13) gave:

$$(5) \quad W(t) = 105.4 e^{-0.000456 \cdot t} \quad (8 \text{ pairs of values})$$

$$r^2 = 0.899***$$

A graphic representation of the function is shown in Figure 10.

The combined hemicellulose fractions (Table 14) gave:

$$(6) \quad W(t) = 105.0 e^{-0.000787 \cdot t} \quad (12 \text{ pairs of values})$$

$$r^2 = 0.961***$$

A graphic representation of the function is shown in Figure 12.

The combined polymer carbohydrate fractions (glucans and hemicelluloses, Table 15) gave:

$$(7) \quad W(t) = 99.4 e^{-0.000101 \cdot t} \quad (10 \text{ pairs of values})$$

$$r^2 = 0.905***$$

A graphic representation of the function is shown in Figure 10.

The weight losses from the fractions apparently followed the type of functions tested for. Even if, in some cases, such as the lignin and the glucan fractions there are relatively few measured pairs of values and somewhat lower r^2 values they still are acceptable for the type function. For the lignin fraction a straight line function also appears reasonable and a regression analysis test for a straight line gave the r^2 value of 0.863. This line is not represented in the figure, however.

The Klason lignin fraction contains both true lignin and humic substances - the former possibly being decomposed also in early stages and the latter being built up. Only a net process has been measured and the function suggested only gives the net changes of an analytical fraction. A rather complex situation is thus at hand and can give

a good illustration that background facts should be taken into consideration before accepting a function. It is quite possible that the decomposition of the other components also is more complicated than a simple weight loss.

It appears that despite the reasonable suggestion by Minderman (1968) that weight loss functions for single litter components should be investigated such an investigation should be carried out with care. Weight losses of single components were not independent on each other and the functions should thus be affected. The closeness to the type function e^{-x} was higher for the whole litter with r^2 -values of 0.986 and 0.990 (section 3.3), and for the combined hemicelluloses with 0.961. For the single components tested the values were 0.897 for arabinans, 0.959 for mannans, 0.823 for glucans and 0.826 for extractives.

The answer to the question in the heading would thus be - so far - "yes, but single chemical components could follow other functions".

3.5 A budget for needle litter in the L layer

The budget calculations were only carried out for the L layer, the aim being to give the amounts of needle litter biomass and some main flows in the L layer. The calculations were carried out from the yearly inputs of needle litter (Flower-Ellis, pers. comm.) with the assumption that 10 per cent of the litter fall takes place in May (May 1) and 90 per cent in October (October 1). The amount of needle litter stored in the L layer and its chemical components were taken from Staaf & Berg (1977).

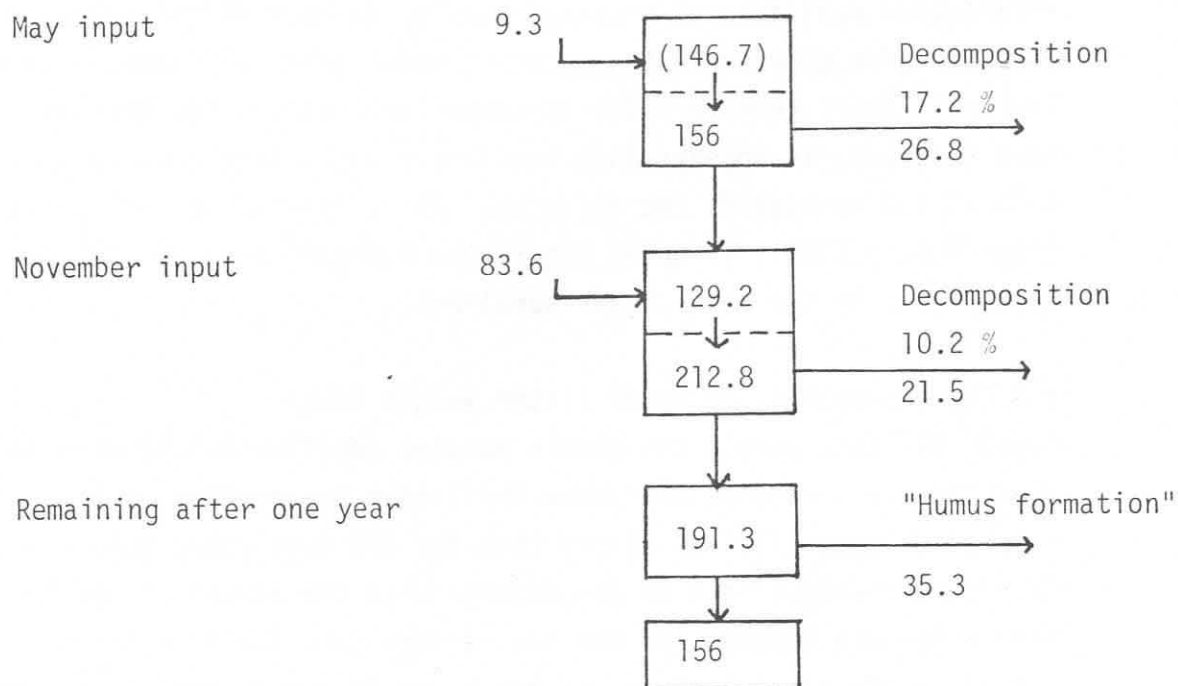
The weight losses of the needle litter and its chemical components are taken from section 3.2.4. As in earlier budget calculations (Berg, 1977), a steady state was assumed for the forest stand and the soil layers so that there are no significant changes between years.

In the years 1974, 1975 and 1976 the needle litter-falls were 96.6, 101.9 and 80.1 g/m^2 (Flower-Ellis, pers. comm.) respectively with the average of 92.9 g/m^2 . The one-year long litter-fall period studied started after the end of the intensive needle litter-fall in October and thus ran from November to November.

Two samplings of the litter and humus in L and FH layers were carried out, namely in May 1974 and early September 1975 with the measured amounts of 156 and 149 g/m² of needle litter respectively in the L layer (Staafl & Berg, 1977).

Weight loss values were the applicable averages from the series A, B, C and D for the periods May to November and November to May as listed in Table 16.

The L layer litter compartment as measured in May contained 156 g/m². As this compartment was measured after snow melt the needle litter input from November to May was considered to have taken place already (cf. figure below)./



Changes in the L layer litter compartment in a year. Sorts are in g/m² unless otherwise indicated.

The decomposition from May to November was 17.2 per cent thus releasing 26.8 g of litter per m². In November the new input of 83.6 g was added to the compartment, thus increasing it to 212.8 g/m². With the winter decomposition of 10.2 per cent we would have 191.3 g left in May. With the assumption of a steady state we have an excess of 35.3 g/m² in the

needle litter compartment which thus ought to have entered into a non-identifiable form. When calculating the theoretical yearly humus formation from the litter input and weight loss figures for each single year I obtained the figures of 34, 53 and 32 g/m². It should be remembered, however, that the assortment procedure might give rise to an underestimate of the litter compartment for the L layer causing an overestimate in the calculated amount of humus formed (Staaf & Berg, 1977).

A calculation of the amount of humus which would be stored in the L layer at steady state was carried out. The yearly weight loss value of 28.1 per cent was used and the amount of 35.3 g of humus formed. The constant fraction weight loss concept was applied (cf. Section 3.3) and under these conditions about 120-130 g/m² of humus originating from needle litter would be stored at a more or less constant level. It is, of course, impossible to control the validity of such a figure with the information available at present. Further decomposition studies could possibly give more correct data which would make calculations more fruitful. Apart from purposes of comparison between two methods (cf. next section), it appears that the figure might have a reasonable magnitude. Thus, as regards the fractions "miscellaneous" as presented by Staaf & Berg (1977) it would contribute 208 g/m² and 259 g/m² for "miscellaneous" in the two L layer samplings.

3.6 The two methods to study litter weight loss

During the same period the needle bundles (section 3.1.1) were decomposed about 76 per cent more than were the litter bag needles. A recalculation of the measured value of 60 per cent for 460 days would then give 46 per cent annual weight loss to be compared with the annual 28 per cent for the litter bag method. For the two periods used for calculation, namely May to November and November to May we would get 28 and 17 per cent respectively. A similar calculation to that shown in the figure would thus give only 9.2 g of humus yearly from the needle litter. The big fraction of "miscellaneous" (208 and 259 g/m² respectively) in the L layer (Staaf & Berg, 1977) did not correspond to the amount of about 20-24 g humus which would be a consequence at a reached steady state with an even addition of 9.2 g of humus and a constant weight loss rate (section 3.3). At steady state the litter bag method gave a figure of 120-130 g/m², which was closer to the value measured.

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Table 1. Weight loss of decomposing needle litter placed on the L and between L and FH layers in the 120-year-old Scots pine stand at Ivantjärnsheden (Ih V). The measurement started on 740502. Weight loss in per cent of initial weight. Standard error for 19 samples within parentheses. Figures given in % of actual weight (A) and in mg g⁻¹ of initial needle litter (B).

Date of sampling	No. of days	Weight loss	Klason lignin		Nitrogen (total)		Nitrogen bound to Klason lignin		Nitrogen not bound to Klason lignin ¹		Cellulose		Hemi-celluloses		Total polymer carbohydrates	
			A	B	A	B	A	B	A	B	A	B	A	B	A	B
Litter layer																
740502	0	0 (-)	22.3	223	0.38	3.8	0.10	0.98	0.28	2.8	19.9	199	15.2	152	35.1	351
751029	545	43.2 (1.1)	40.1	230	0.85	4.8	0.31	1.78	0.51	2.9	22.3	127	21.6	123	43.9	249
760428	726(2 years)	44.4 (0.8)	42.6	236	0.79	4.4	0.29	1.59	0.50	2.8	20.9	116	20.9	116	41.8	232
760825	845	51.2 (1.2)	43.1	210	0.92	4.5	0.34	1.66	0.66	3.2	16.0	78	16.0	78	32.0	156
Between litter and humus layer																
740502	0	0 (-)	22.3	223	0.38	3.8	0.10	0.98	0.28	2.8	19.9	199	15.2	152	35.1	351
751029	545	39.2 (1.1)	41.5	252	0.71	4.7	0.29	1.79	0.41	2.9	25.8	153	18.4	115	44.0	268
760428	726(2 years)	44.3 (1.5)	41.6	232	0.79	4.4	0.35	1.93	0.44	2.5	26.1	145	16.3	91	42.4	236
760825	845	48.1 (1.6)	44.9	233	0.88	4.6	0.39	2.01	0.49	2.7	24.9	129	16.7	87	41.6	216

1) Calculated as difference between total nitrogen and Klason lignin nitrogen.

2) Analysis value from Berg *et al.* (in manuscript).

Table 2. Weight losses from needle litter in litter-bags (A-series) at different locations within the study-site in a 120-years-old Scots pine (*Pinus silvestris*) forest at Ivantjärnsheden.

Days	Location within the site																			Mean value	SE
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
105	13.1	5.7	10.9	15.7	9.2	7.0	14.1	9.1	10.6	9.6	13.5	11.7	9.2	9.2	13.0	19.1	-	0.9	5.5	10.4	0.96
326	24.5	23.7	26.6	26.2	27.0	22.4	25.9	30.9	26.7	21.7	11.5	22.4	26.4	-	19.7	23.4	22.7	28.2	30.0	24.4	1.00
358	32.3	26.0	18.4	29.9	25.9	21.9	26.2	32.9	15.5	30.2	30.9	30.5	23.2	-	31.7	26.2	33.4	30.8	26.2	27.3	1.16
497	41.9	42.5	49.1	42.7	42.4	36.5	39.5	45.2	50.1	38.2	47.2	37.7	31.9	42.6	46.5	44.7	41.0	52.8	46.6	42.9	1.12
679	42.0	43.7	49.3	40.5	46.0	43.1	46.4	45.3	48.8	42.1	48.7	43.4	40.9	37.9	46.0	43.7	47.9	50.1	38.5	44.4	0.83

Table 3. Weight loss changes in needle litter under decomposition in the 120-year-old Scots pine (*Pinus silvestris*) stand at Ivantjärnsheden. Standard error within parenthesis.

Series A				Series B				Series C				Series D			
Date	No of days	Weight loss (%)		Date	No of days	Weight loss (%)		Date	No of days	Weight loss (%)		Date	No of days	Weight loss (%)	
740512	0	0	(0)	741023	0	0	(0)	751029	0	0	(0)	761110	0	0	(0)
740902	123	10.4	(0.23)	750526	212	17.7	(0.31)	760428	182	8.8	(0.10)	770601	232	11.1	(0.43)
741103	185	17.8	(0.89)	750912	323	23.3	(0.40)	760707	252	10.7	(0.20)	770912	297	21.6	(0.30)
750411	344	24.4	(1.00)	751028	370	28.2	(0.59)	760825	302	14.9	(0.27)	771027	352	26.5	(0.55)
750513	366	27.3	(1.16)	760428	554	32.2	(0.42)	761110	379	21.1	(0.38)				
750904	490	35.7	(0.91)	761110	747	42.8	(0.78)	770601	611	31.5	(0.69)				
751029	545	43.2	(1.05)	771027	1099	58.1	(1.60)	771027	728	44.5	(0.69)				
760428	726	44.5	(0.83)												
760825	845	51.2	(1.24)												
761110	922	55.8	(1.19)												
770601	1125	58.8	(1.65)												
770912	1228	63.0	(1.30)												
771027	1273	63.8	(0.88)												

Table 4. Weight loss and some chemical changes in needle litter in decomposition measurements in a 120-year-old stand of Scots pine (*Pinus silvestris*) at Jädraås. Series A, start 740512.

	Date of sampling	No. of days	Weight loss (%)	Standard error	Remaining litter of 1000 mg litter (mg)	Total carbon (%)	Total nitrogen (%)	Amount of carbon in remains from 1000 mg litter (mg)	Amount of nitrogen in remains from 1000 mg litter (mg)	Klason lignin (%)	Amount of lignin in remains from 1000 mg litter (mg)	Nitrogen bound to Klason lignin (%)
1.	740512 (start)	0	0	-	1000	51.1 ¹	0.38	511	3.80	22.3 ²	223	0.44
2.	740902	123	10.4	0.23	896	52.3 ¹	0.37	469	3.32	24.9 ²	223	0.50
3.	741103	185	17.8	0.89	822	52.9 ¹	0.48	435	3.95	28.3 ²	233	0.61
4.	750411	344	24.4	1.00	756	51.1 ¹	0.59	386	4.46	n.d.	n.d.	0.74
5.	750513	366	27.3	1.16	727	51.1 ¹	0.62	371	4.51	33.1 ²	241	0.74
6.	750904	490	35.7	0.91	643	51.9 ¹	0.76	334	4.92	36.3	235	0.74
7.	751029	545	43.2	1.05	568	51.8 ¹	0.85	294	4.83	40.1 ²	230	0.83
8.	760428	726	44.4	0.83	556	n.d.	0.79	n.d.	4.39	42.6 ²	236	0.75
9.	760825	845	51.2	1.24	488	n.d.	0.92	n.d.	4.49	43.1	210	0.79
10.	761110	922	55.8	1.19	442	52.6	0.99	232	4.38	46.8	207	1.02
11.	770601	1125	58.8	1.65	412	n.d.	0.96	n.d.	3.96	n.d.	n.d.	n.d.
12.	770912	1228	63.0	1.30	370	n.d.	1.02	n.d.	3.77	44.0	168	1.05
13.	771027	1273	63.8	0.88	362	n.d.	1.18	n.d.	4.27	43.8	159	0.94

1) Staaf, pers. comm.

2) Berg, Hannus, Popoff and Theander, in manuscript

Table 4, continued

	Amount of Klason lignin nitrogen in remains from 1000 mg litter	Nitrogen not bound to Klason lignin	Amount of nitrogen not bound to Klason lignin in remains from 1000 mg litter	Glucans	Remaining glucans from 1000 mg litter	Mannans	Remaining mannans from 1000 mg litter	Galactans	Remaining galactans from 1000 mg litter	Arabinans
	(mg)	(%)	(mg)	(%)	(mg)	(%)	(mg)	(%)	(mg)	(%)
1.	0.98	0.28	2.82	19.9 ²	199	5.9 ²	59	2.8 ²	28	4.0 ²
2.	1.12	0.25	2.20	23.7 ²	212	6.5 ²	58	3.1 ²	28	3.1 ²
3.	1.40	0.31	2.55	29.4 ²	242	8.2 ²	67	3.1 ²	25	2.6 ²
4.	n.d.	n.d.	n.d.	28.4	215	7.8	59	4.1	31	2.6
5.	1.78	0.38	2.73	27.4 ²	199	8.1 ²	59	2.9 ²	21	2.3 ²
6.	1.74	0.50	3.18	30.0	195	8.3	53	4.1	26	2.8
7.	1.78	0.51	2.92	22.3 ²	127	8.5 ²	48	3.4 ²	19	5.0 ² (2.6)
8.	1.59	0.50	2.80	20.9 ²	116	7.9 ²	44	3.1 ²	17	5.5 ² (2.5)
9.	1.66	0.66	3.23	16.0 ²	78	6.0 ²	29	3.4 ²	17	2.8 ²
10.	2.11	0.54	2.37	17.4 ²	77	6.8 ²	30	3.0 ²	13	3.4 ²
11.	n.d.	n.d.	n.d.	n.d.	-	n.d.	-	n.d.	-	n.d.
12.	1.76	0.54	2.01	22.1	83	5.7	21	3.4	13	2.3
13.	1.49	0.77	2.78	23.2	83	6.2	22	4.0	14	2.3

Table 4, continued

	Remaining arabinans from 1000 mg litter (mg)	Xylans (%)	Remaining xylans from 1000 mg litter (mg)	Rhamnans (%)	Remaining rhamnans from 1000 mg litter (mg)	Hemicelluloses (%)	Remaining hemicelluloses from 1000 mg litter (mg)	Total polymer carbohydrate (%)
1.	40	2.1 ²	21	7 ²	7	15.2 ²	155	34.2 ²
2.	27	2.5 ²	22	5 ²	5	15.7 ²	141	39.4 ²
3.	22	2.1 ²	17	5 ²	4	16.5 ²	136	45.9 ²
4.	20	n.d.	-	5	4	17.9	135	46.3
5.	17	2.1 ²	15	5 ²	4	15.9 ²	116	43.3 ²
6.	18	3.4	22	5	3	19.5	125	49.6
7.	28 (15)	4.4 ²	25	3 ²	1	21.6 ² (19.2)	123 (109)	43.9 ² (41.5)
8.	31 (14)	3.5 ²	19	9 ²	5	20.9 ² (17.9)	116 (100)	41.8 ² (38.8)
9.	14	2.5 ²	12	13 ²	6	16.0 ²	78	32.0 ²
10.	15	3.1 ²	14	11 ²	5	17.4 ²	77	34.8 ²
11.	-	n.d.	-	n.d.	-	n.d.	-	n.d.
12.	8	3.6	13	7	3	15.7	58	37.8
13.	8	3.4	12	9	3	16.8	61	40.0

Table 4, continued

	Remaining polymer carbohydrates from 1000 mg litter (mg)	Water solubles (%)	Remaining water soluble from 1000 mg litter (mg)	Acetone solubles (%)	Remaining acetone solubles from 1000 mg litter (mg)	Total extractives (%)	Remaining extractives from 1000 mg litter (mg)	Ash (%)	Remaining ash from 1000 mg litter (mg)
1.	342	9.2 ²	92	12.0	120	27.2 ²	272	2.3	23
2.	353	11.6 ²	104	n.d.	n.d.	28.6 ²	256	n.d.	-
3.	377	12.5 ²	103	n.d.	n.d.	28.8 ²	237	n.d.	-
4.	350	5.4	41	9.6	73	15.0	113	2.1	16
5.	315	9.7 ²	71	8.4	61	22.2 ²	161	2.6	19
6.	319	4.5	29	8.2	53	12.7	82	2.6	17
7.	249 (236)	4.9	28	8.4	48	15.0 ²	85	2.4	14
8.	232 (216)	4.4(5.9)	24	8.5(8.8)	47	17.1 ² (14.7)	95(82)	2.1	12
9.	156	9.0(5.4)	44	6.0(9.4)	29	16.0 ² (14.8)	78(72)	2.4	12
10.	154	3.3(4.6)	15	7.4(8.5)	33	13.2 ² (13.1)	58(58)	2.7	12
11.	-	n.d.	-	n.d.	-	n.d.	-	n.d.	-
12.	140	6.0	22	10.0	37	16.0 (14.0)	59 (52)	2.8	10
13.	145	4.7	17	11.4	41	16.1	58	2.7	10

Table 5. Weight loss and some chemical changes in needle litter in decomposition measurements in a 120-year-old stand of Scots pine (*Pinus silvestris*) at Jädraås. Series B, start 741023.

	Date	Days	Weight loss	Standard error	Remaining litter of 1000 mg	Total carbon	Total nitrogen	Amount of carbon in remains from initially 1000 mg	Amount of nitrogen in remains from initially 1000 mg	Klason lignin	Amount of lignin in remains from 1000 mg litter	Nitrogen bound to Klason lignin
			(%)		(mg)	(%)	(%)	(mg)	(mg)	(%)	(mg)	(%)
1.	741023 (start)	0	0	-	1000	50.5	0.42	505	4.20	27.0	269.8	0.56
2.	750526	212	17.7	0.31	823	51.0	0.46	420	3.79	35.2	290.0	0.59
3.	750912	323	23.3	0.40	767	50.3	0.49	386	3.76	35.8	274.7	0.60
4.	751028	370	28.2	0.59	718	49.7	0.53	357	3.80	34.8	250.0	0.54
5.	760428	554	32.2	0.42	678	n.d.	0.56	-	3.79	35.4	239.7	0.56
6.	761110	747	42.8	0.78	572	50.4	0.71	-	4.06	37.5	214.4	0.77
7.	771027	1099	58.1	1.60	419	n.d.	0.99	-	4.15	42.2	177.0	0.88

Table 5, continued

	Amount of Klason lignin nitrogen in remains from 1000 mg litter	Nitrogen not bound to Klason lignin (%)	Amount of nitrogen not bound to Klason lignin in remains from 1000 mg litter (mg)	Glucans (%)	Remaining glucans from 1000 mg litter (mg)	Mannans (%)	Remaining mannans from 1000 mg litter (mg)	Galactans (%)	Remaining galactans from 1000 mg litter (mg)	Arabinans (%)	Remaining arabinans from 1000 mg litter (mg)
1.	1.51	0.27	2.69	29.9	299	8.4	84	3.9	39	3.8	38
2.	1.71	0.25	2.08	33.2	273	8.6	71	3.8	32	2.8	23
3.	1.65	0.28	2.11	32.9	252	8.7	67	3.8	29	2.8	21
4.	1.35	0.34	2.45	32.8	236	8.4	60	3.8	27	2.7	19
5.	1.34	0.36	2.45	32.8	222	8.7	59	3.8	26	2.6	18
6.	1.65	0.42	2.41	29.6	169	7.0	40	5.4	31	2.6	15
7.	1.56	0.62	2.59	25.3	106	6.6	28	3.4	14	2.9	12

Table 5, continued

	Xylans	Remaining xylans from 1000 mg litter	Rhamnans	Remaining rhamnans from 1000 mg litter	Hemicelluloses	Remaining hemi- celluloses from 1000 mg litter	Total polymer carbo- hydrate	Remaining polymer carbo- hydrates from 1000 mg litter	Water solubles	Remaining water solubles from 1000 mg litter
	(%)	(mg)	(%)	(mg)	(%)	(mg)	(%)	(mg)	(%)	(mg)
1.	2.6	26	0.4	4.0	19.2	192	49.1	491	14.5	145.0
2.	2.8	23	0.5	3.3	18.5	152	51.7	425	6.4	52.7
3.	3.2	24-25	0.5	3.8	19.0	146	51.9	398	5.2	39.9
4.	3.1	22	0.5	3.6	18.5	133	51.3	368	5.3	38.1
5.	3.5	24	0.5	3.4	19.1	129	51.9	352	5.8	39.3
6.	2.8	16	0.4	2.3	18.2	104	47.8	273	4.6	26.3
7.	3.5	15	0.7	2.9	17.1	72	42.3	177	6.1	25.6

Table 5, continued

	Acetone solubles	Remaining acetone solubles from 1000 mg litter	Total extractives	Remaining extractives from 1000 mg litter	Ash	Remaining ash from 1000 mg litter
	(%)	(mg)	(%)	(mg)	(%)	(mg)
1.	8.4	84.0	22.9	229.0	2.4	24
2.	5.6	46.0	12.0	98.8	2.7	22
3.	5.8	44.5	11.0	84.4	2.5	19
4.	7.0	50.3	12.3	88.3	2.5	18
5.	6.4	43.4	12.2	82.7	2.5	17
6.	7.3	41.8	11.9	68.1	2.5	14
7.	9.3	39.0	15.4	64.5	2.5	10

Table 6. Plot values taken from the graph in Fig. 1 (series A) for the plotting of a first order kinetics' process as presented in Fig. 9.

Time (days)	$\frac{C_o}{C_t}$	$\ln 10 \cdot \log \frac{C_o}{C_t}$
0	1.000	0.0000
100	1.087	0.0834
200	1.188	0.1723
300	1.289	0.2539
400	1.404	0.3387
500	1.520	0.4188
600	1.639	0.4942
700	1.773	0.5728
800	1.916	0.6504
900	2.075	0.7301
1000	2.252	0.8120
1100	2.427	0.8868
1200	2.591	0.9522

Table 7. Plot values taken from the graph in Fig. 2 (series B) for the plotting of a first order kinetics' process presented in Fig. 2.

Time (days)	$\frac{C_0}{C}$	$\ln 10 \times \log \frac{C_0}{C}$
0	1.0000	0.0000
100	1.1086	0.1031
200	1.1876	0.1719
300	1.2987	0.2614
400	1.4085	0.3426
500	1.5060	0.4095
600	1.6077	0.4748
700	1.7123	0.5379
800	1.8349	0.6071
900	1.9802	0.6833
1000	2.1552	0.7680
1100	2.3697	0.8629

Table 8. Rate constants and time for weight loss to 50%, 90% and 99% for *Pinus silvestris* needle litter in a 120-year-old stand at Ivantjärnsheden. Series A and B.

	Rate constant $10^3 \cdot \text{day}^{-1} \text{ yr}^{-1}$		50% weight loss yrs	90% weight loss yrs	99% weight loss yrs
Series A (graphic calculation from Fig. 3).	0.81	0.297	2.33	7.8	16
Series A (13 measurements) ¹⁾	0.79	0.288	2.28	7.9	16
Series B (7 measurements) ¹⁾	0.75	0.274	2.48	8.4	17
Series A (4 measurements) ¹⁾	0.78	0.285	2.39	8.0	16
Series B (4 measurements) ¹⁾	0.77	0.281	2.42	8.2	16

1) Thirteen and seven measurements refer to all samplings and start value whereas four measurements refer to three samplings with one-year intervals and start value.

Table 9. Weight loss from the "total extractives" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was: $C(t) = 84.76 e^{-0.001284 \cdot t}$. Shown in Figure 10.

From start of experiment (days)	Time	Remaining amount (C(t)) (% of initial)	Amount decomposed (%)	Function plot values	
	From day when components net weight loss started (days)			Time (days)	Weight loss (%)
0	0	100.0	0.0	0	84.76
123	123	94.1	5.9	100	74.57
185	185	87.1	12.9	200	65.56
344	344	41.5	58.5	300	57.66
366	366	59.2	40.8	400	50.71
490	490	30.1	69.9	500	44.60
545	545	31.3	68.7	600	39.22
726	726	30.1	69.9	700	34.50
845	845	28.7	71.3	800	30.34
922	922	21.3	78.7	900	26.68
1 125	1 125	-	-	1 000	23.47
1 228	1 228	21.7	78.3	1 100	20.64
1 273	1 273	21.3	78.1	1 200	18.15
				1 300	15.96

Table 10. Weight loss from the "arabinans" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was $C(t) = 75.6 e^{-0.000103 \cdot t}$. Shown in Figure 11.

From start of experiment (days)	Time		Remaining amount (C(t)) (% of initial)	Amount decomposed (%)	Function plot values	
	From start of experiment (days)	From day when components net weight loss started (days)			Time (days)	Remaining amount (C(t)) (%)
0	0	0	100.0	0	0	75.6
123	123	123	67.5	32.5	100	68.2
185	185	185	55.0	45.0	200	61.5
344	344	344	50.0	50.0	300	55.5
366	366	366	42.5	57.5	400	50.1
490	490	490	45.0	55.0	500	45.2
545	545	545	37.5	62.5	600	40.7
796	796	796	35.0	65.0	700	36.8
845	845	845	35.0	65.0	800	33.2
922	922	922	37.5	62.5	900	29.9
1 125	1 125	1 125	-	-	1 000	27.0
1 228	1 228	1 228	20.0	80.0	1 100	24.3
1 273	1 273	1 273	20.0	80.0	1 200	22.0
					1 300	19.8

Table 11. Weight loss from the "mannans" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was $C(t) = 100.9 e^{-0.001180 \cdot t}$, shown in Figure 12.

From start of experiment (days)	Time	Remaining amount (% of initial)	Amount decomposed (%)	Function plot values	
	From day when components net weight loss started (days)			Time (days)	Remaining amount $C(t)$ (%)
0	no weight loss	100.0	0.0	0	100.9
123	"	100.0	0.0	100	89.7
185	"	100.0	0.0	200	79.7
344	"	100.0	0.0	300	70.9
366	0	100.0	0.0	400	63.0
490	124	89.8	10.2	500	56.0
545	179	81.4	18.6	600	49.8
726	360	74.6	25.4	700	44.2
845	479	49.2	50.8	800	39.3
922	556	50.8	49.2	900	34.9
1 125	759	-	-	1 000	31.1
1 228	862	35.6	74.4	1 100	27.6
1 273	907	37.3	72.7	1 200	24.5

Table 12. Weight loss from the "glucans" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was: $C(t) = 94.2 e^{-0.001130 \cdot t}$, shown in Figure 11.

From start of experiment (days)	Time		Remaining amount (% of initial)	Amount decomposed (%)	Function plot values	
	From start of experiment (days)	From day when components net weight loss started (days)			Time (days)	Remaining amount $C(t)$ (%)
0		no weight loss	100.0	0.0	0	94.2
123		"	100.0	0.0	100	84.1
185		0	100.0	0.0	200	75.2
344		159	88.8	11.2	300	67.1
366		181	82.2	17.8	400	60.0
490		305	80.6	19.4	500	53.6
545		360	52.5	47.5	600	47.8
726		541	47.9	52.1	700	42.7
845		660	32.2	67.8	800	38.2
922		737	31.8	68.2	900	34.1
1 125		940	-	-	1 000	30.4
1 228	1 043		34.3	65.7	1 100	27.2
1 273	1 085		34.3	65.7	1 200	24.3
					1 300	21.7

Table 13. Weight loss from the "Klason lignin" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was: $C(t) = 105.4 e^{-0.000456 \cdot t}$, shown in Figure 10.

Time		Remaining amount (% of initial)	Amount decomposed (%)	Function plot values	
From start of experiment (days)	From day when components net weight loss started (days)			Time (days)	Remaining amount $C(t)$ (%)
0	no weight loss	100.0	0.0	0	105.4
123	"	100.0	0.0	100	100.7
185	"	100.0	0.0	200	96.2
344	"	100.0	0.0	300	91.9
366	0	100.0	0.0	400	87.8
490	124	97.5	2.5	500	83.9
545	179	95.4	4.6	600	80.2
726	360	97.9	2.1	700	76.6
845	479	87.1	12.9	800	73.2
922	556	85.9	14.1	900	69.9
1 125	759	-	-	1 000	66.8
1 228	862	69.7	30.3	1 100	63.8
1 273	907	66.0	44.0	1 200	61.0
				1 300	58.3

Table 14. Weight loss from the "total hemicelluloses" fraction of the needle litter, series A. Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was: $C(t) = 105.0 e^{-0.000787 \cdot t}$, shown in Figure 12.

From start of experiment (days)	Time		Remaining amount (% of initial)	Amount decomposed (%)	Function plot values	
	From start of experiment (days)	From day when components net weight loss started (days)			Time (days)	Remaining amount $C(t)$ (%)
0	0	0	100.0	0.0	0	105.0
123	123	123	91.0	9.0	100	97.0
185	185	185	87.7	12.3	200	89.7
344	344	344	87.1	12.9	300	82.9
366	366	366	74.8	25.2	400	76.6
490	490	490	80.6	19.4	500	70.8
545	545	545	70.3	29.7	600	65.5
726	726	726	64.5	35.5	700	60.5
845	845	845	50.3	49.7	800	56.0
922	922	922	49.7	50.3	900	51.7
1 125	1 125	1 125	-	-	1 000	47.8
1 228	1 228	1 228	37.4	62.6	1 100	44.2
1 273	1 273	1 273	39.4	60.6	1 200	40.8
					1 300	37.8

Table 15. Weight loss from the "total polymer carbohydrates" fraction of the needle litter, series A.
Regression analysis values from the function obtained from values of time and remaining amount. Function obtained was: $C(t) = 99.4 e^{-0.000101 \cdot t}$, shown in Figure 10.

From start of experiment (days)	Time	Remaining amount (% of initial)	Amount decomposed (%)	Function plot values	
	From day when components net weight loss started (days)			Time (days)	Remaining amount (C(t) (%))
0	no weight loss	100.0	0.0	0	99.4
123	"	100.0	0.0	100	89.8
185	0	100.0	0.0	200	81.2
344	159	92.8	7.4	300	73.5
366	181	83.6	16.4	400	66.4
490	305	84.6	15.4	500	60.1
545	360	62.6	37.4	600	54.3
726	541	57.3	42.7	700	49.1
845	660	41.4	58.6	800	44.4
922	737	40.8	59.2	900	40.2
1 125	940	-	-	1 000	36.3
1 228	1 043	37.1	62.9	1 100	32.8
1 273	1 088	38.5	61.5	1 200	29.7
				1 300	26.9

Table 16. Weight loss from Scots pine needle litter in the 120-year-old Scots pine stand at Ivantjärnsheden. Series A-D. The listed values were used for budget calculations (section 3.5).

		Series A		Series B		Series C		Series D		Average for the periods
		Weight loss from ini- tial (%)	Weight loss in period from pre- vious uptake (%)	Weight loss from ini- tial (%)	Weight loss in period from pre- vious uptake (%)	Weight loss from ini- tial (%)	Weight loss in period from pre- vious uptake (%)	Weight loss from ini- tial (%)	Weight loss in period from pre- vious uptake (%)	
1974	May	0	0	-	-	-	-	-	-	0
	Nov.	17.8	17.8	0	0	-	-	-	-	17.8
1975	May	27.3	11.6	17.7	17.7	-	-	-	-	14.7
	Nov.	43.2	21.9	28.2	12.8	0	0	-	-	17.4
1976	May	44.5	2.3	32.2	5.6	8.8	8.8	-	-	5.5
	Nov.	55.8	20.4	42.8	15.6	21.1	13.5	0	0	16.5
1977	May	58.8	6.8	-	-	31.5	13.2	11.1	11.1	10.4

The average for May to November was 17.2 per cent
The average for November to May was 10.2 per cent

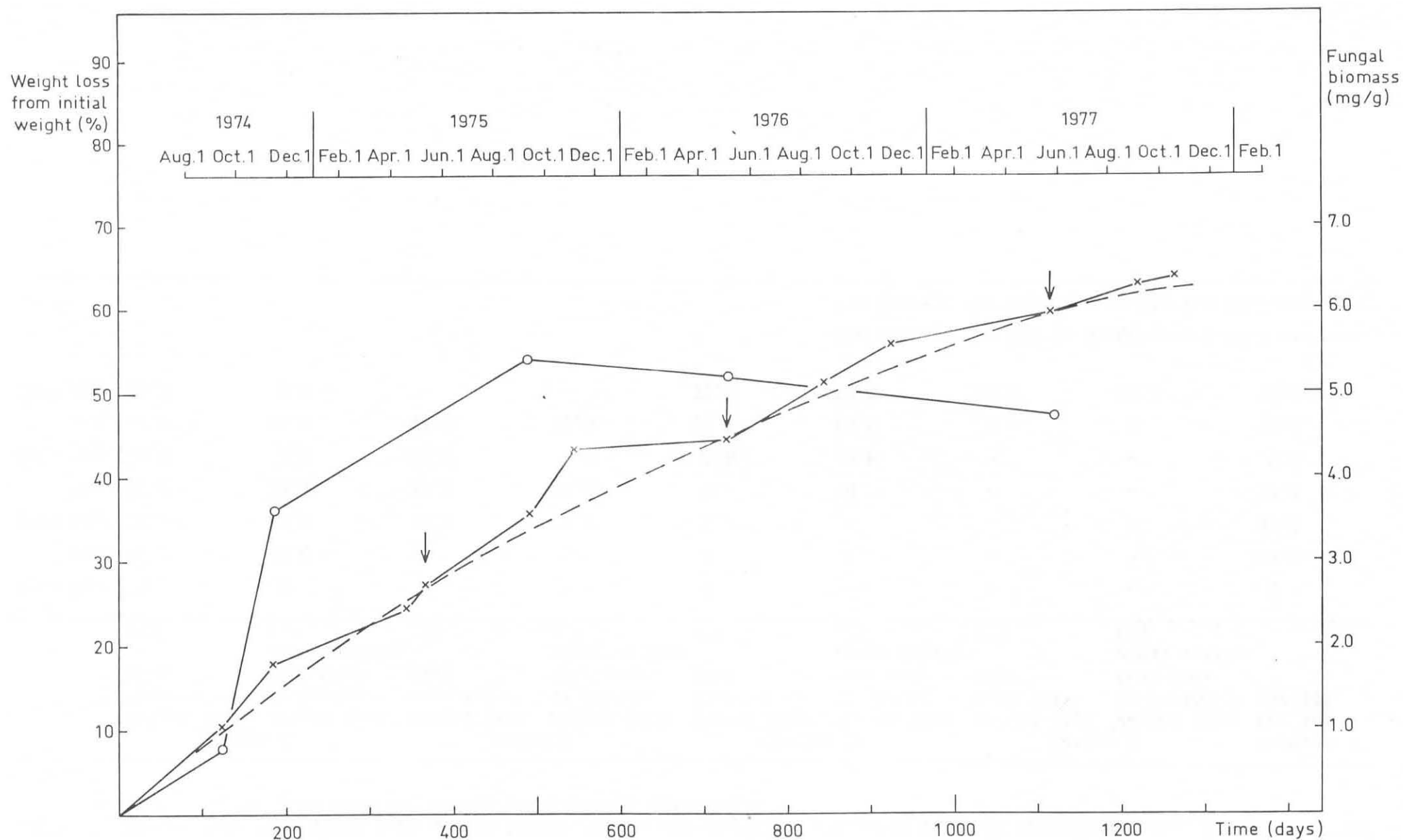


Figure 1. Weight loss from initial weight of Scots pine needle litter in a measurement started 740512 (A-series) in a 120-year-old stand at Ivantjärnsheden, Jädraås. Biomass of fungal mycelium (Berg and Söderström, in manuscript) is indicated. The arrows indicate weight loss values after 1, 2 and 3 years' decomposition. The following symbols are used: x — x — x for weight loss; o — o — o for fungal biomass. The dashed line combines the 1, 2 and 3 year weight loss values.

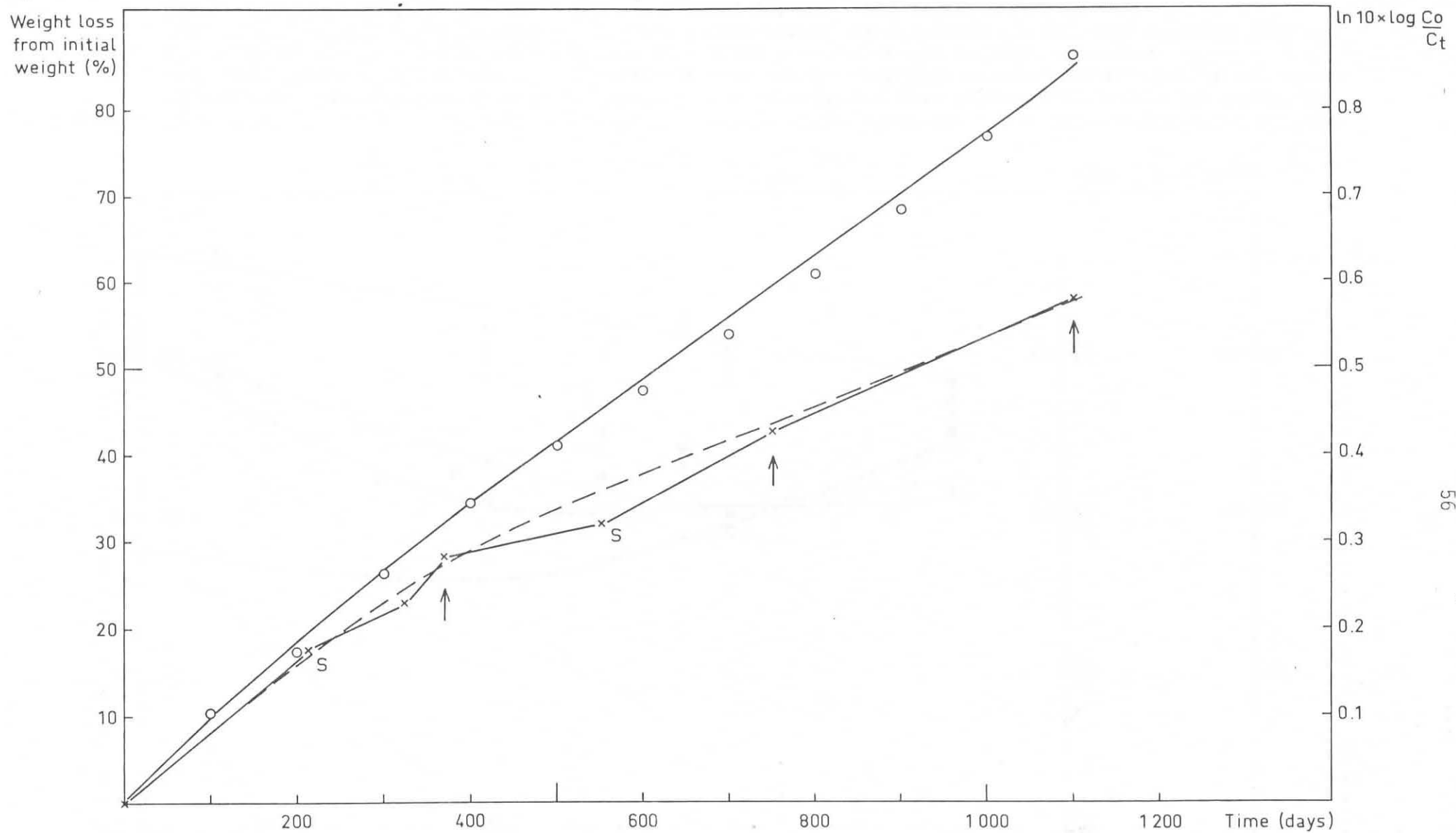


Figure 2. Weight loss from initial weight of Scots pine needle litter in a measurement started 741023 (B-series) in a 120-year-old stand at Ivantjärnsheden, Jädraås. A plotting of the weight loss as a process of first order kinetics is shown. The arrows indicate the weight loss values after 1, 2 and 3 years' decomposition and the spring samplings are indicated with the letter S. The following symbols are used: x — x — x for weight loss; o — o — o for the kinetic plot. The dashed line combines the 1, 2 and 3 year weight loss values.

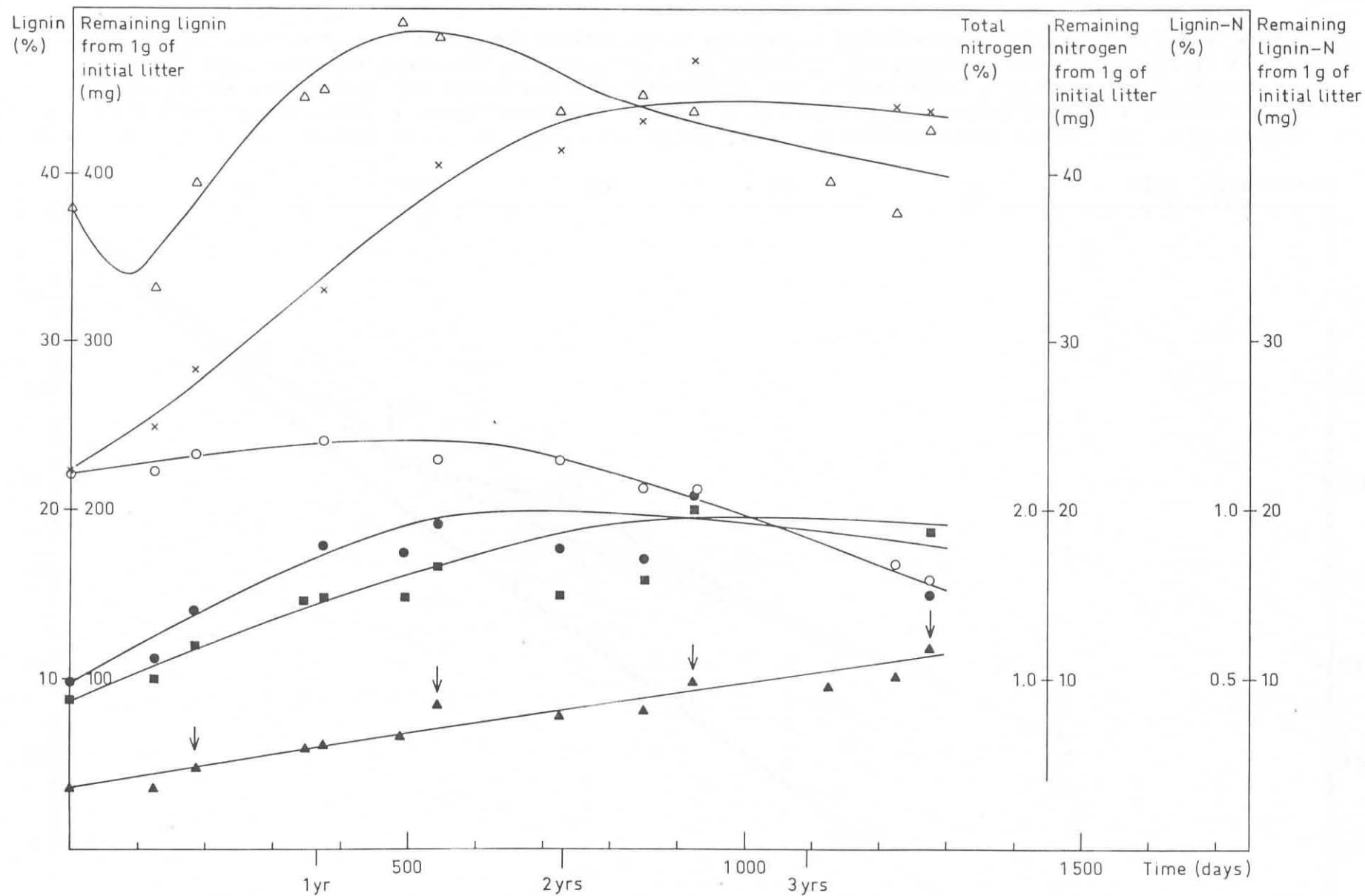


Figure 3. Some chemical changes in decomposing Scots pine needle litter (A-series) in a 120-year-old stand at Ivan-tjärnsheden. The following symbols are used: x — x — x for per cent lignin; o — o — o for amount of remaining lignin from 1 g initial litter; ■ — ■ — ■ for per cent lignin-nitrogen; ● — ● — ● for amount of remaining lignin-nitrogen from 1 g initial litter; ▲ — ▲ — ▲ for per cent nitrogen; Δ — Δ — Δ for amount of remaining nitrogen from 1 g initial litter. Arrows at the graph for per cent nitrogen indicate the late autumn sampling. One, two, and three years are indicated at the time axis.

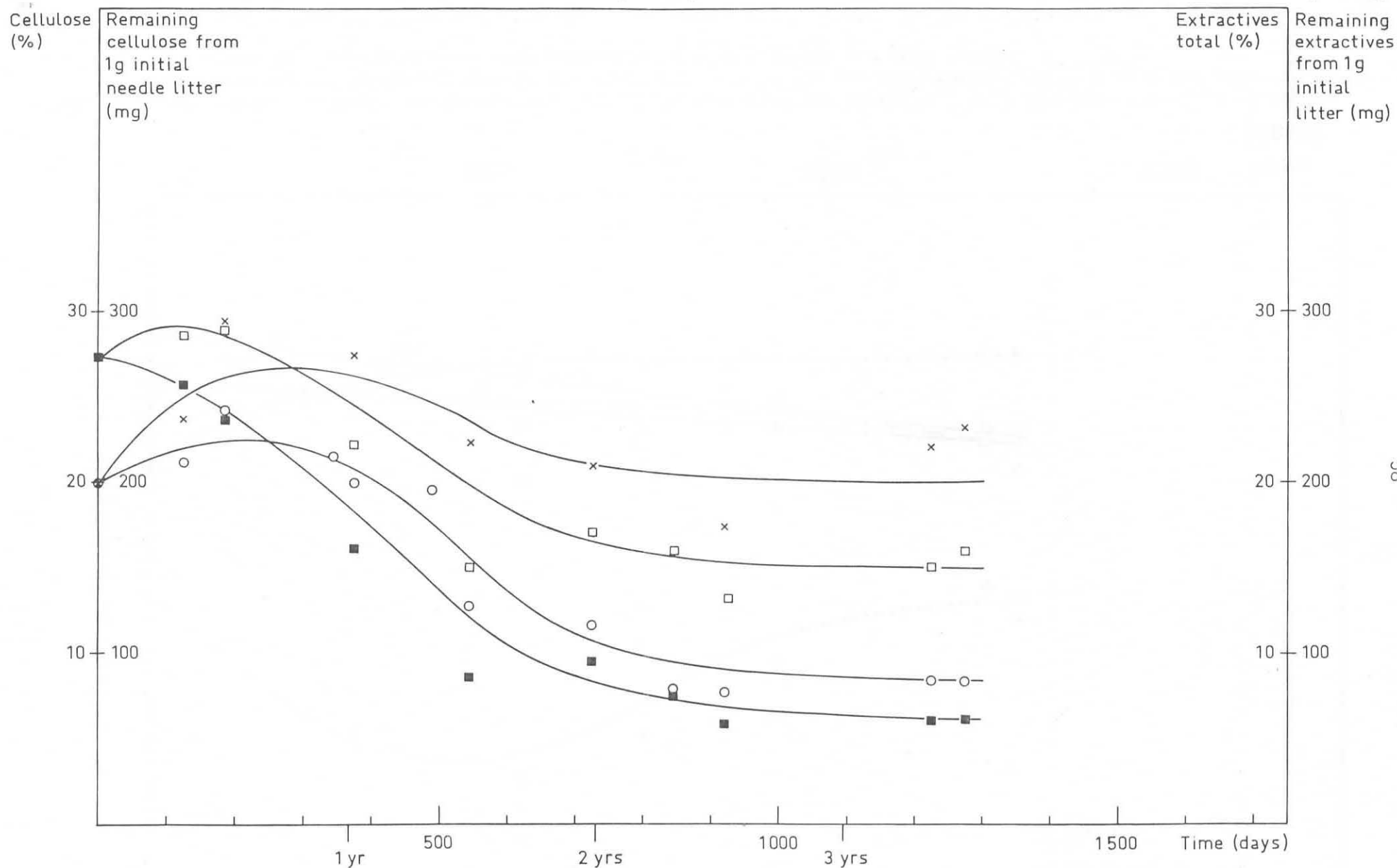


Figure 4. Changes in percentage and content of cellulose and extractives (water and acetone) in decomposing pine needle litter (A-series) in a 120-year-old stand at Ivantjärnsheden. The following symbols are used: x — x — x for per cent cellulose; o — o — o for amount of remaining cellulose from 1 g initial litter; □ — □ — □ for per cent total extractives; ■ — ■ — ■ for amount of remaining extractives from 1 g initial litter.

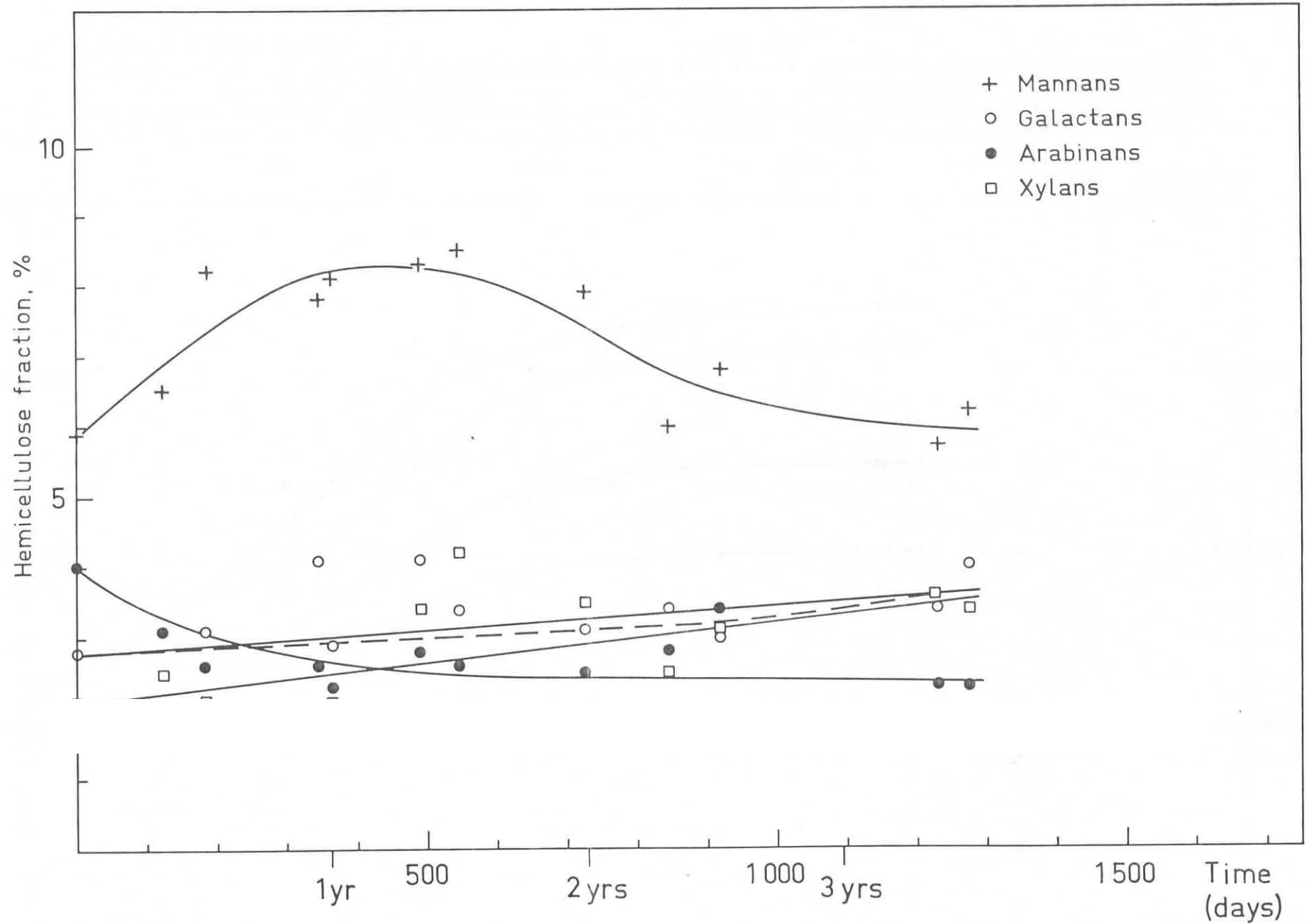


Figure 5. Some chemical changes in decomposing Scots pine needle litter (A-series) in a 120-year-old stand at Ivan-tjärnsheden. The following symbols are used; + — + — + for per cent mannans; o — o — o for per cent galactans; ● — ● — ● for per cent arabinans; □ — □ — □ for per cent xylans.

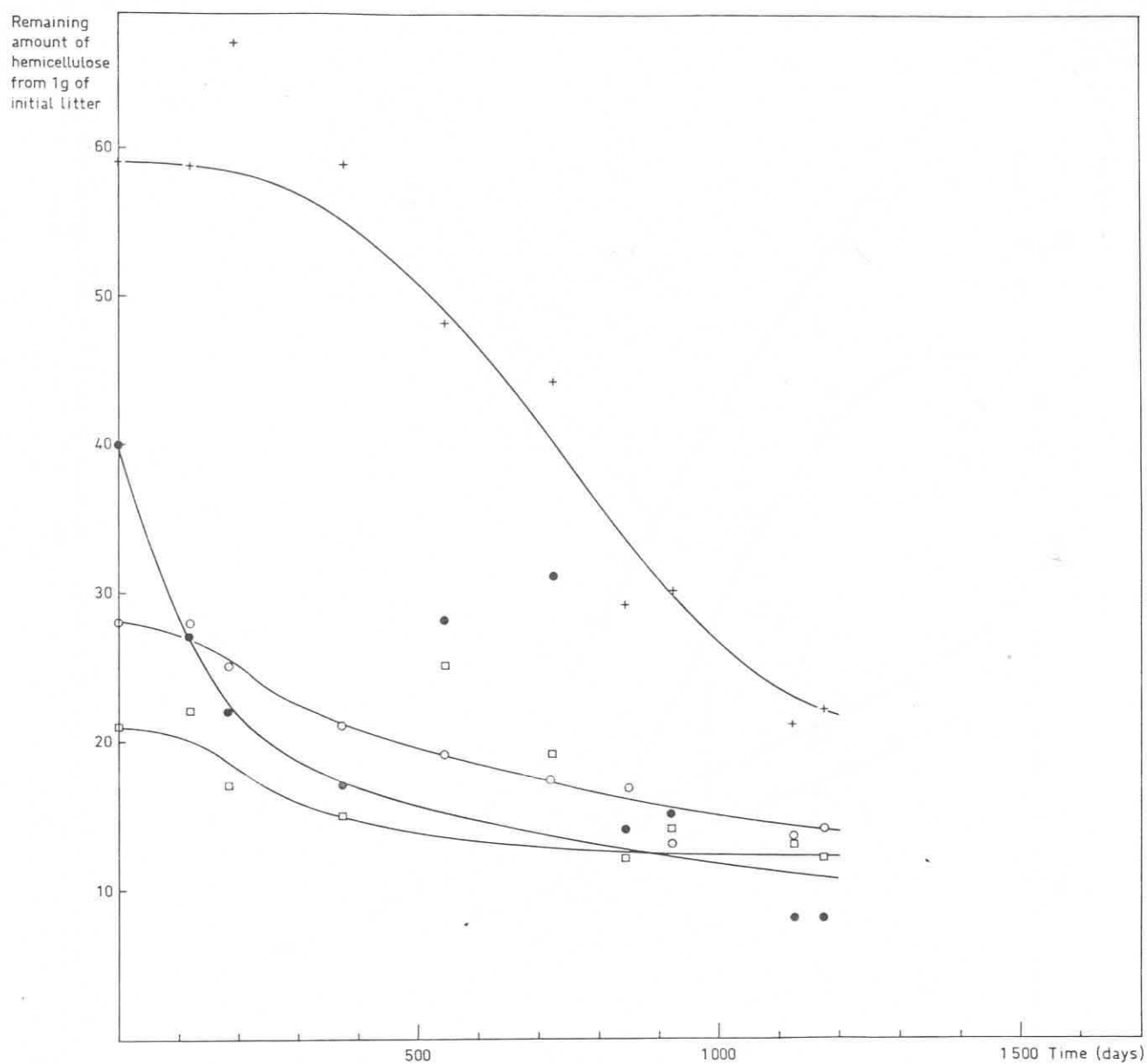


Figure 6. Some chemical changes in decomposing Scots pine needle litter (A-series) in a 120-year-old stand at Ivantjärnsheden. The following symbols are used: + — + — + for remaining amount of mannan from 1 g initial litter; o — o — o for remaining amount of galactan from 1 g of initial litter; • — • — • for remaining amount of arabinan from 1 g of initial litter; □ — □ — □ for remaining amount of xylan from 1 g of initial litter.

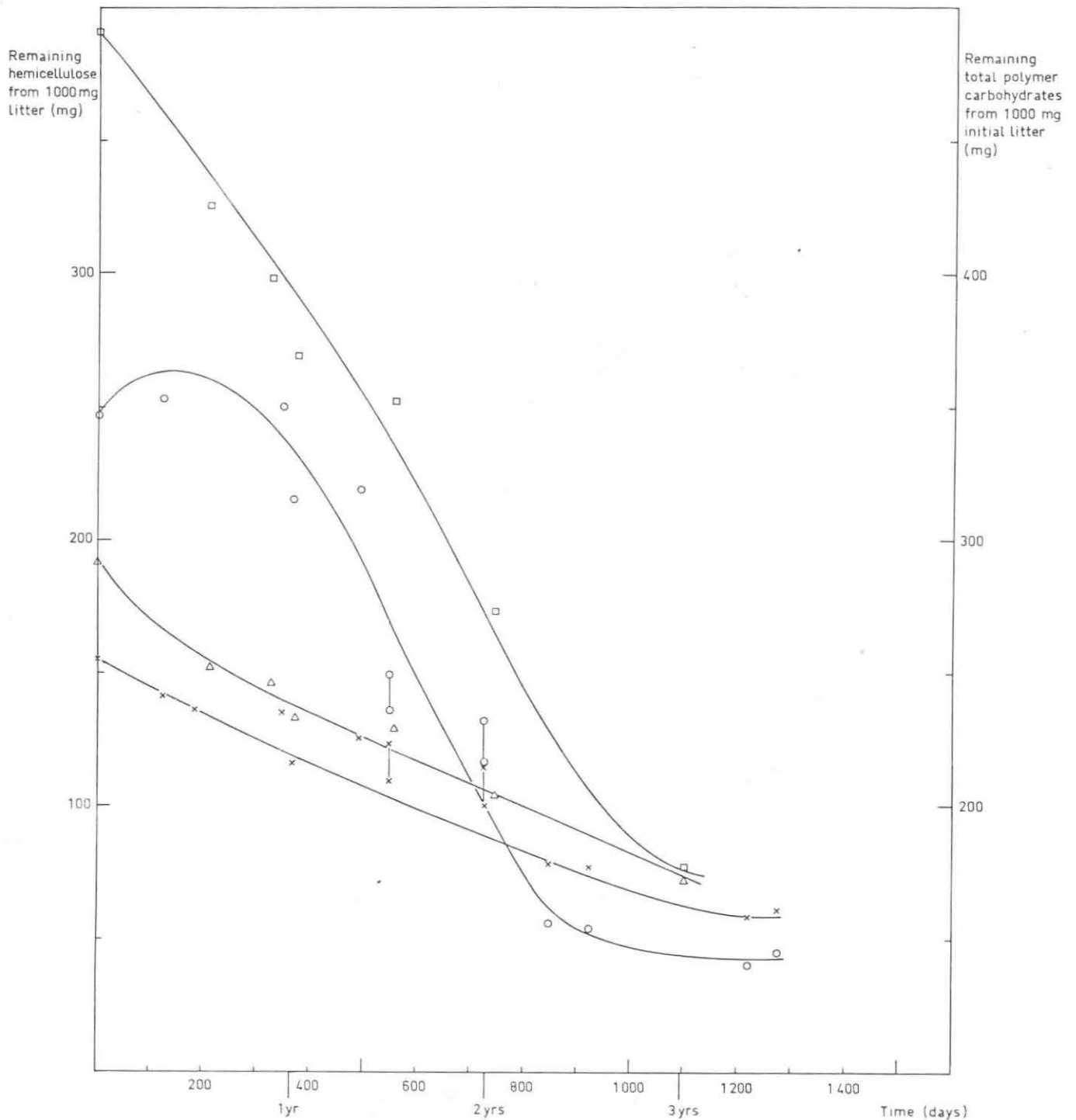


Figure 7. Some chemical changes in decomposing Scots pine needle litter (A and B series) in a 120-year-old stand at Ivantjärnsheden. Weight loss from the total polymer carbohydrate fraction and the fraction of combined hemicelluloses. The following symbols are used: x — x — x for remaining amount of hemicelluloses (A-series); o — o — o for remaining amount of total polymer carbohydrates (A-series); Δ — Δ — Δ for remaining amount of hemicelluloses (B-series); □ — □ — □ for remaining amount of total polymer carbohydrates (B-series).

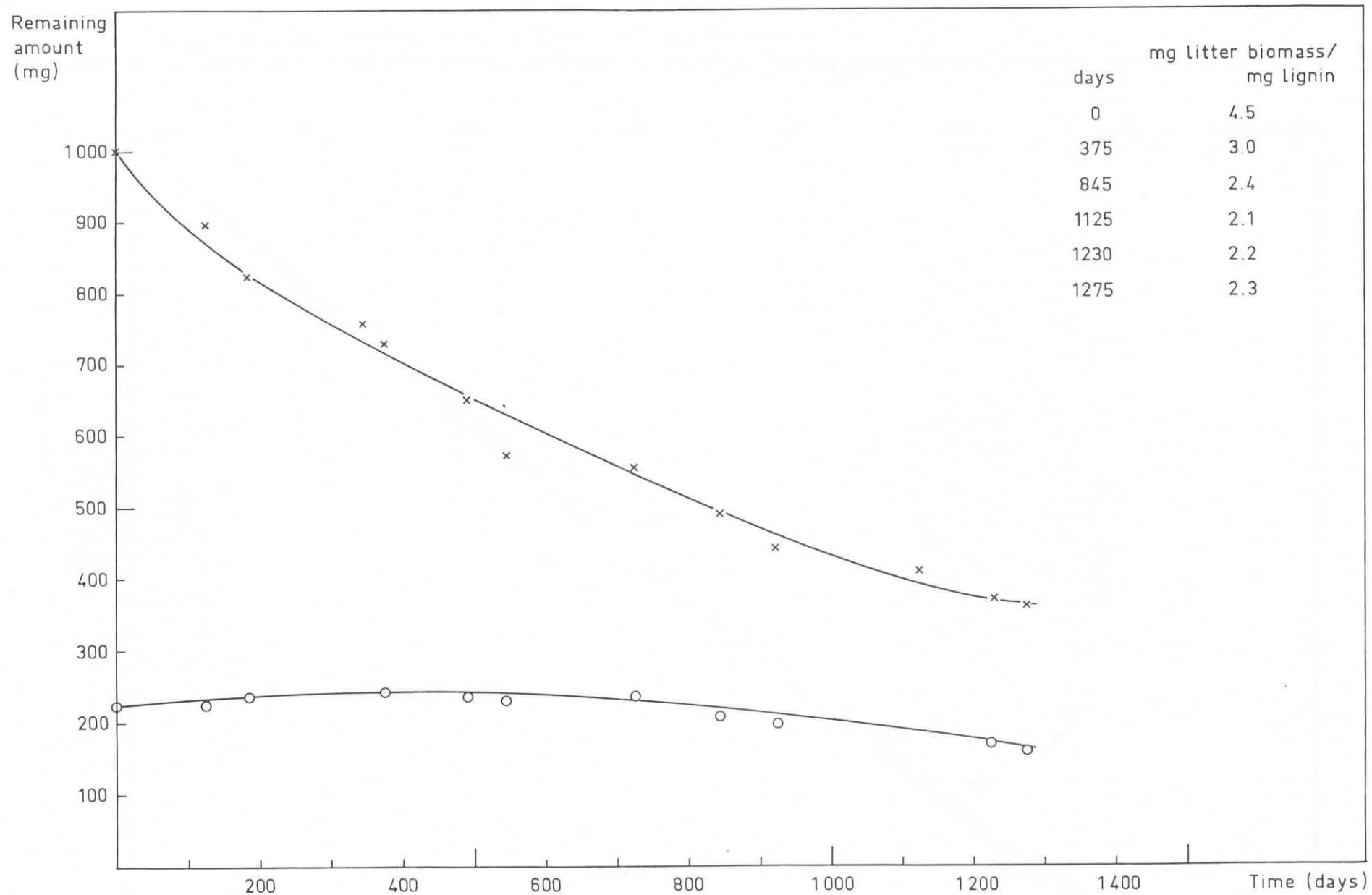


Figure 8. The relation between total remaining litter weight and remaining lignin in decomposing Scots pine needle litter in a 120-year-old stand at Ivantjärnsheden, Jädraås (A-series). The following symbols are used: x — x — x for total remaining litter; o — o — o for remaining lignin.

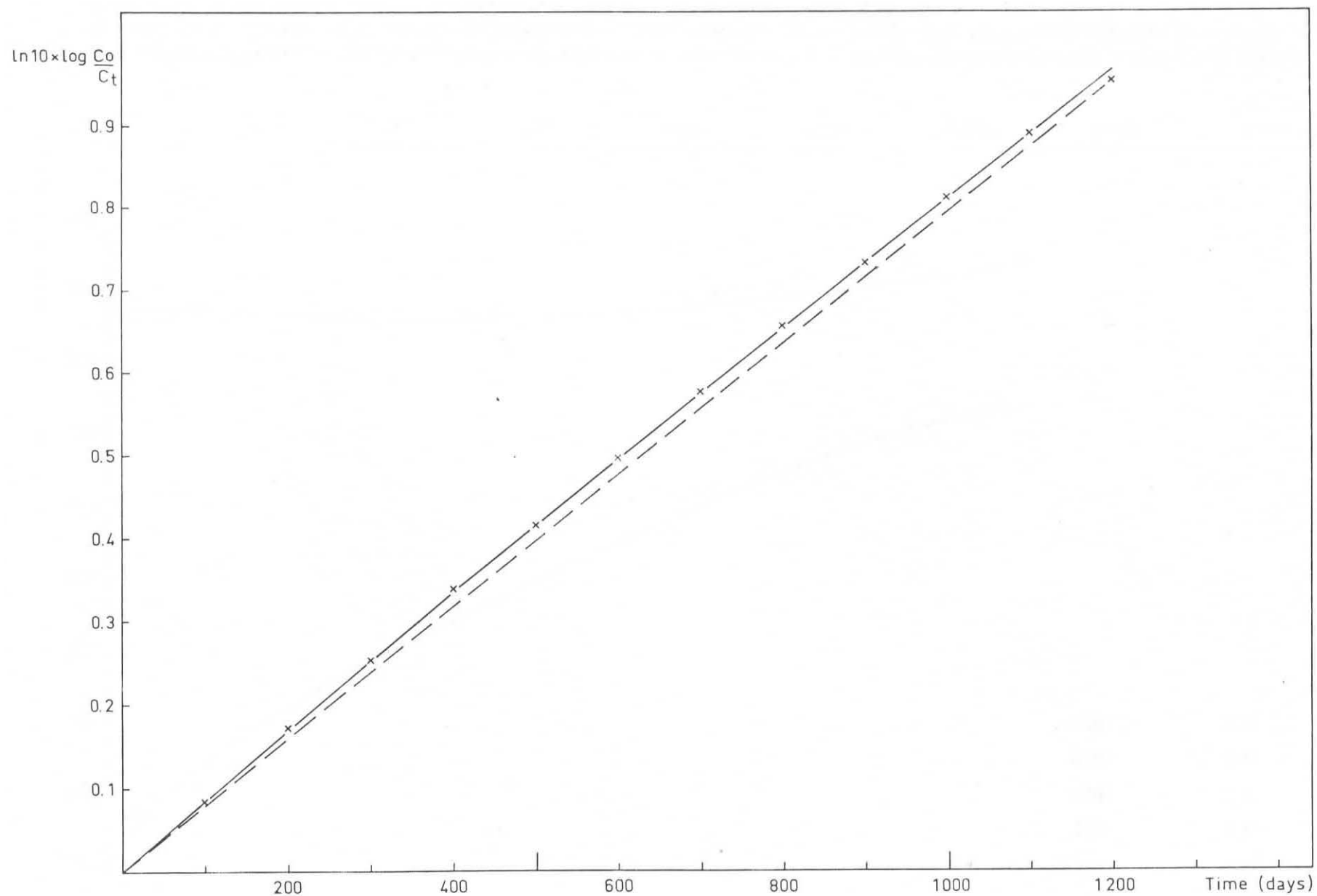


Figure 9. Plotting of weight loss values from Fig. 1 as a process of first order kinetics. The dashed line is a straight line drawn to show the graph's slight curvature.

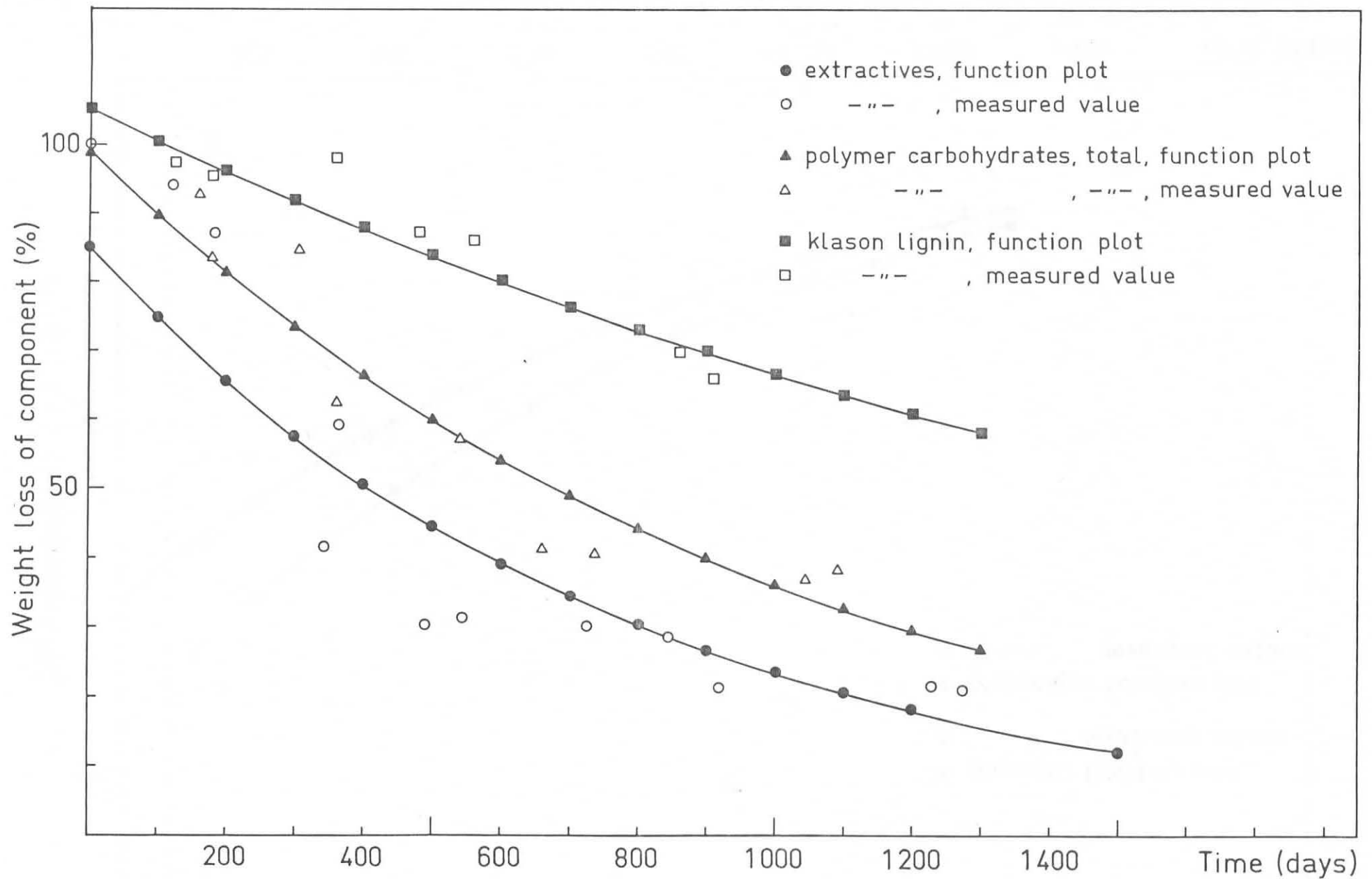


Fig. 10. Graphic representation of calculated functions for the weight losses of some of the organic components in Scots pine needle litter; Klason lignin, total extractives, and total polymer carbohydrates. Measured values are also indicated. Time axis gives time from the day decomposition started for the component. Symbols as presented in figure.

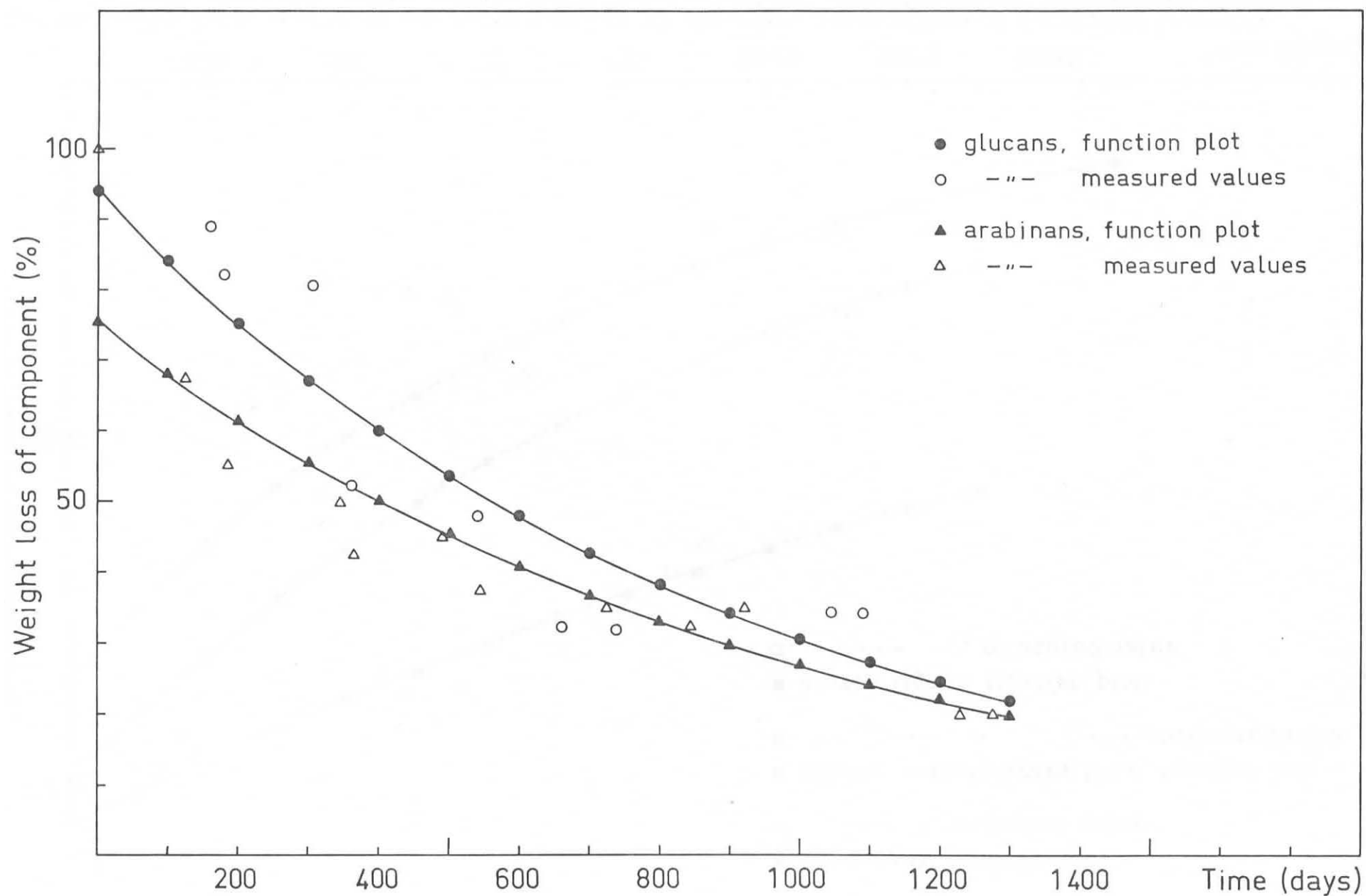


Figure 11. Graphic representation of calculated functions for the weight losses of some of the organic components in Scots pine needle litter: glucans and arabinans. Measured values are also indicated. Time axis gives time from the day decomposition started for the component. Symbols as presented in figure.

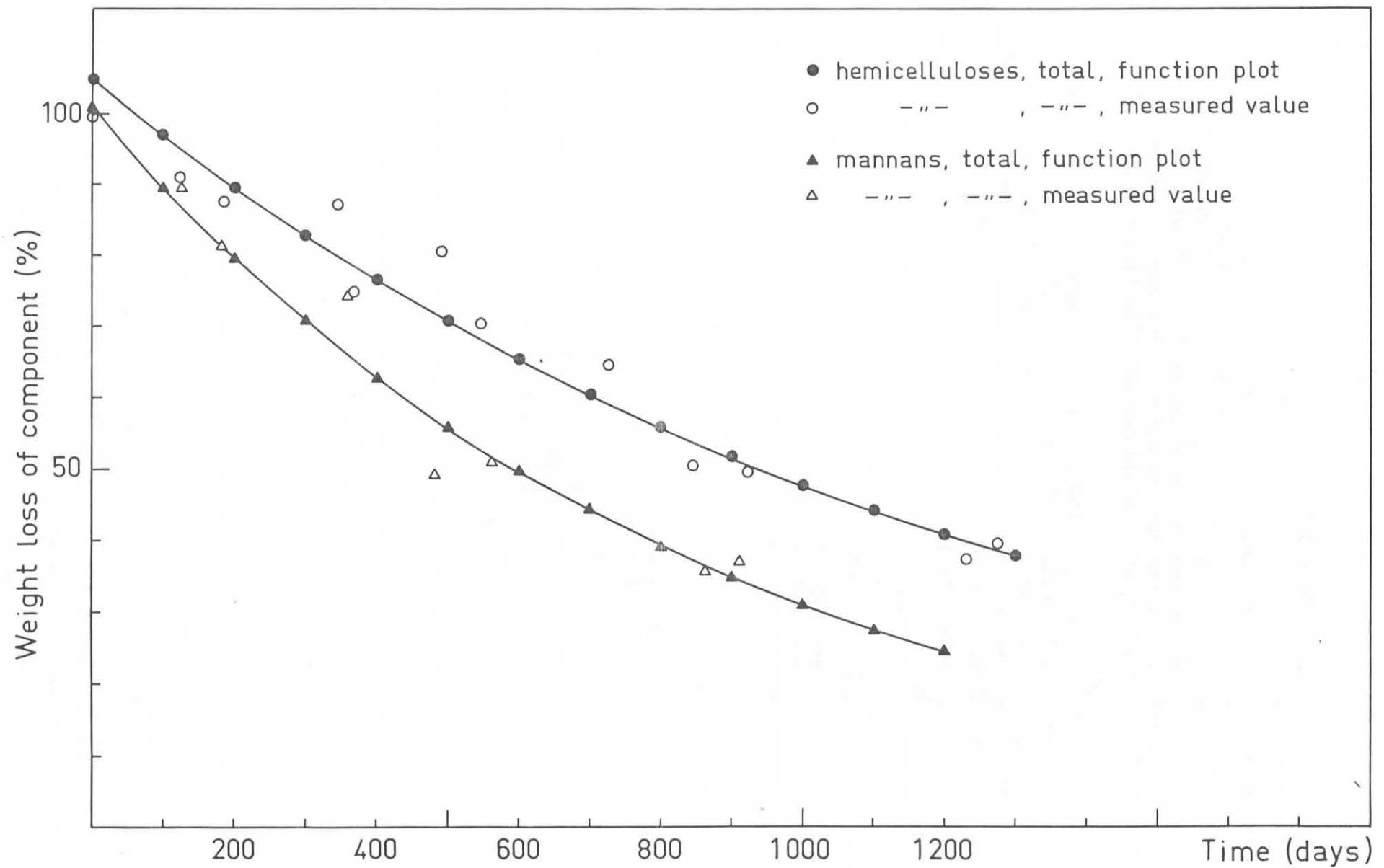


Figure 12. Graphic representation of calculated functions for the weight losses of some of the organic components in Scots pine needle litter; total hemicelluloses and mannans. Measured values are also indicated. Time axis gives time from the day decomposition started for the component. Symbols as presented in figure.